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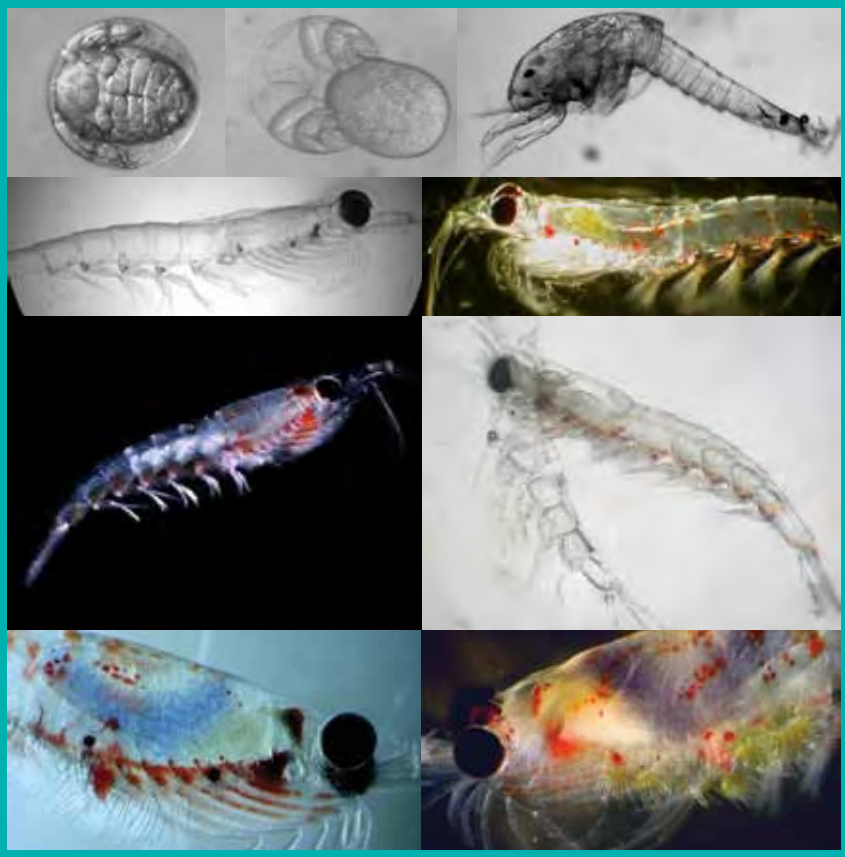

Report of Working Group 23 on Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim

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Report of Working Group 23 on Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim

Edited by
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Contents

Executive Summary

In October 2007, the PICES Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* (WG 23) was established under the direction of the Biological Oceanography Committee (BIO) with the following terms of reference:

1. Assemble lists of existing data (including metadata) that contribute to an analysis of the comparative ecology of *Euphausia pacifica* and *Thysanoessa* species. Identify gaps in our understanding of krill ecology, life history, and population dynamics.
2. Prepare a research plan to help fill gaps in our understanding and aid regional collaborative research efforts. Explore ways and means of facilitating exchange of scientists between laboratories and on research cruises.
3. Convene "hands-on" practical workshops with krill biologists (including students and established scientists) from PICES member countries to help them initiate and carry out krill research programs. Workshops could be convened before PICES meetings, or at other times as appropriate. A protocol for experimental work has already been published on the PICES website at: http://www.pices.int/projects/Euphasiid/PICES%20Protocols%20COMPLETE.pdf.
4. Initiate euphausiid research programs in PICES member countries which will include sampling on a regular basis (biweekly-monthly) to determine seasonal cycles of spawning and growth, and incubations of live animals for measurement of brood size and molting rates.
5. Work with modelers to better parameterize euphausiids in the NEMURO and other models so as to explore their role in coastal and oceanic food chains.
6. Convene a krill workshop at the GLOBEC Open Science Meeting (May 2009).
7. Organize a Krill Symposium or a Topic Session at PICES XX in 2011, and submit a set of krill synthesis papers for a special issue of a scientific peer-reviewed journal.

This report brings together reviews of the state of knowledge of *Euphausia pacifica* and *Thysanoessa* species in the six PICES member countries over the time period from 2008 to 2012. The chances to conduct euphausiid research varied amongst countries, but PICES scientists rose to the challenge and made the most of the opportunities available to them. From mining euphausiid data out of existing time-series data sets to conducting live euphausiid experiments (using the protocol available on the PICES website, http://www.pices.int/projects/Euphasiid/euphasiid.aspx), WG 23 members generated new and interesting data on euphausiids throughout the North Pacific. Although we were not able to convene the hands-on workshop proposed in TOR #3, scientists from Chile, China, Japan, and Germany were able to travel to Newport, Oregon to work in the laboratory led by Dr. William (Bill) Peterson located at the Hatfield Marine Science Center, NOAA-Fisheries, and members of the Peterson lab visited China to work with Chinese colleagues and Korea to participate in several research cruises in the Yellow Sea. These international collaborations involved experiments on live euphausiids, including molting and growth rates, egg production, feeding preferences and rates, and effects of hypoxia.

WG 23 organized a workshop on "*Krill biology and ecology in the world's oceans*" in conjunction with the GLOBEC Open Science Meeting in Victoria, Canada, in June 2009. The objective of the workshop was to convene a gathering of krill biologists and ecologists from around the world to discuss the life history and population dynamics of all krill species. The workshop was well attended and included presentations on euphausiid research from 11 countries (the UK, Germany, Australia, Peru, Chile, Mexico, USA, Canada, Japan, China and Korea). Discussion of euphausiid research from these many geographic locations yielded several common themes:

- current biomass calculations for all krill species are probably underestimates,
- the roles of krill as both a predator and a prey item are not well understood,
- there is a need to better understand krill behaviour, especially in regard to swarming,
- there is a need for more pan-oceanic research to understand the impact of climate variability on krill ecology and production.

In addition, we learned about promising results related to krill population dynamics using IBM models linked with ROMS (Regional Ocean Model System). These model results show how euphausiid eggs (from broadcast spawners) and larvae are transported by interactions between currents and ontogenetic variations in vertical distribution.

A special issue on krill biology and ecology was published in Deep-Sea Research Part II (Vol. 57, Issues 7–8) in April 2010. This special issue was developed following the workshop "*Krill research: current status and its future*" that took place in conjunction with the 4th International Zooplankton Production Symposium in Hiroshima, Japan in 2007. Guest editors were Drs. So Kawaguchi and William T. Peterson and the special issue was dedicated to the memory of Dr. Edward Brinton. The volume comprises 17 original research papers from scientists in eight countries: Australia, Chile, China, Japan, Korea, Mexico, the UK, and the USA.

Looking beyond WG 23

At the final meeting of WG 23 in Khabarovsk, Russia, in 2011, it was clear from the presentations and discussion that there is still much more to be done on this topic and that some of our findings and work could serve as the basis for establishing a new working group. We identified two topics that merit further attention and that would make substantial contributions to defining the role of euphausiids (and other zooplankton) in the marine environment. One of these topics is euphausiid vital rates, including seasonal growth rates, lifetime fecundity, and mortality rates. This information would improve our current models and enable us to predict with greater accuracy how euphausiids will be affected by changing environmental conditions. This, in turn, will lead to more accurate assessments of the potential effects of environmental change on higher tropic levels. The other topic considered as the basis for a potential working group is a basin-scale comparison of the role of small pelagics in ecosystems (krill, anchovies, sardines, *etc*.) and how these might be modified by a changing climate. Both of these topics are relevant within the context of the current PICES integrative science program on **F**orecasting and **U**nderstanding **T**rends, **U**ncertainty and **R**esponses of North Pacific Marine **E**cosystems (FUTURE).

Potential subjects for a new zooplankton working group were discussed at PICES-2012 in Hiroshima, Japan, during the workshop on "*Secondary production: Measurement methodology and its application on natural zooplankton community*". Based on this discussion, we determined that a working group on zooplankton production would address many of the criteria of interest. Currently, zooplankton production is usually determined using direct measurements such as molting rate experiments. These methods are laborious and time consuming, and the results are not always conclusive. Biochemical approaches to measuring zooplankton production have the potential to provide quick measurements using simple protocols, but need to be calibrated with direct measurements in order to facilitate comparisons amongst the different methods. We propose to conduct an exchange program to cross-calibrate biochemical methods of measuring zooplankton production and growth (using a nucleic acids ratio, AARS, chitobiase, *etc*.) and validate these methods in relation to traditional methods (direct growth, molting rate, egg production, physiological rate, *etc*.). Aspects of zooplankton biomass and species composition are relevant to researchers involved with modeling and monitoring, as well as scientists associated with PICES' Biological Oceanography Committee, Fishery Science Committee and Technical Committee on Monitoring, but little attention is given to "rates" of growth and production. Since rates are likely to be more sensitive to environmental changes than "biomass", changes in rates could be excellent early indicators of responses to environmental change by the zooplankton community. The ability to make rapid assessments of changes in these rates has the potential to be a useful tool in elucidating the consequences of environmental change for the zooplankton community. We suggest that the

FUTURE Advisory Panels on *Climate, Oceanographic Variability and Ecosystems* (COVE) and *Status, Outlooks, Forecasts, and Engagement* (SOFE) would be interested in incorporating a better understanding of zooplankton growth and production rates into (a) understanding the effects of climate variability on ecosystems (COVE) and (b) outlooks and ecosystem status (SOFE). A proposed PICES working group on zooplankton production would clarify (1) methods of measurements of rates, and (2) recommend a set of techniques that could be adopted by scientists of both PICES and ICES member countries.

Prospective activities of the new working group would include:

1. Reviewing advantages and disadvantages of the current methodologies for zooplankton production;
2. Championing an international research program to compare methodologies (including proposals for funding);
3. Establishing a cooperative network between the PICES working group on zooplankton production and ICES working group on zooplankton ecology;
4. Contributing to the updating of the ICES Zooplankton Methodology Manual (1st Edition) on methods of measuring zooplankton production.

Recommended Steering Committee for the new working group:
Rubén Escribano (IIO)
Hyung-Ku Kang (KIOST)
Toru Kobari (KUFF)
William T. Peterson (NOAA)
Akash Sastri (UQAM)
Lidia Yebra (IEO)

1 Introduction

Euphausiids are a key component of ecosystems throughout the North Pacific. The species *Euphausia pacifica* has a pan-Pacific distribution and is generally the dominant species of euphausiid in most of the waters it inhabits (Brinton, 1962). Euphausiids of the genus *Thysanoessa* are the next most common, though their ranges are more geographically restricted. The fact that *E. pacifica* are found throughout the waters of all PICES member countries and the interest in whether data from various studies could provide insight into how this one species thrives in such a wide variety of ecosystems was the impetus for the establishment of the Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* (WG 23). This final report from WG 23 contains summary reports from each PICES member country that highlight past and ongoing research on euphausiids (Section 3). Most countries do not have research projects specifically targeting euphausiids, so the data come from a variety of other sampling efforts which makes the amount of data available even more remarkable. Data from the North Pacific Continuous Plankton Recorder (CPR) survey (Section 4) are presented separately from the summary reports since they comprise samples from the waters of several PICES member countries. Modeling efforts used to parameterize euphausiids and explore their role in coastal and open-ocean food chains are discussed in Section 5. The last section highlights other successful activities of WG 23, including international collaborations and a protocol for conducting live experiments on euphausiids. The membership of WG 23 throughout its active period is listed in Appendix 1. The appendices also include a set of equations for converting among the different methods of measuring euphausiid length (Appendix 2) and an example of the questionnaire distributed to krill experts internationally (Appendix 3). More details of the working history of WG 23 can be found in its Annual Reports (Appendix 4) and the PICES Press article about the Krill Biology and Ecology Workshop held during the 2009 GLOBEC Open Science Meeting (Appendix 5).

1.1 A Proposal for the Formation of a Working Group on Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim

Euphausiids are among the most important links in coastal and oceanic food webs, transferring energy from primary and secondary producers to higher trophic level animals such as salmon, herring, sardines, mackerel, Pacific whiting, sablefish, many rockfish species, auklets, shearwaters and whales. Given their importance in the food chain, euphausiids may be considered keystone sentinel species. One species of euphausiid, *Euphausia pacifica*, is of special interest because it ranges from the cool upwelling regions off Mexico's Baja California peninsula, California, Oregon, Washington, and British Columbia, into the downwelling environment of the Gulf of Alaska, and across the Pacific through the Transition Zone, then south through the western Pacific from Russia to China. In the western Pacific this species inhabits waters where temperatures range from sub-arctic (*e.g.*, the Oyashio and Bering Sea slope waters) to the sub-tropical (*e.g.*, the Kuroshiro, the East China and Yellow seas). There are few species that occupy such a wide variety of ecosystems and such a wide range of latitudes. Thus, we ask, "What are the unique characteristics of the life history of this cosmopolitan euphausiid species that allow it not only to populate but dominate such a wide variety of ecosystems?"

Surprisingly little information is available on the seasonal cycles of abundance, feeding, and reproduction, or on the growth rates of this species.

Comparative studies are needed to understand their trophic status, their adaptations which allow them to prosper in so many different regions, and to learn how climate change may affect their population dynamics. Given that many scientists within PICES have made great progress in applying NEMURO (**N**orth Pacific **E**cosystem **M**odel for **U**nderstanding **R**egional **O**ceanography) and EcoSim models to the study of ecosystem dynamics, they would benefit greatly from better estimates of euphausiid biomass and vital rates so as to properly parameterize the euphausiid component of these models. Improvements to the models will result in a tool that will allow us to investigate quantitatively the role of euphausiids in food chain dynamics.

PICES scientists are also uniquely capable of increasing our understanding of euphausiids because many oceanographic stations and monitoring lines are routinely sampled for hydrography and zooplankton. With some instructions and basic supplies, sampling of euphausiids could be easily incorporated into these existing monitoring programs to allow the collection of living animals at night to make measurements of reproduction, molting and growth rates.

Studies which focus on this single species, *Euphausia pacifica*, will provide a common starting point for international exchanges and partnerships. Scientists from PICES member countries have information and experience to share, and all would benefit from an increased understanding of this species. Moreover, scientific exchanges involving research cruises or visits to laboratories will further foster an exchange of ideas and will promote long-term collaborations among students as well as established research scientists.

Terms of Reference

1. Assemble lists of existing data (including metadata) that contribute to an analysis of the comparative ecology of *Euphausia pacifica* and *Thysanoessa* species. Identify gaps in our understanding of krill ecology, life history and population dynamics.
2. Prepare a research plan to help fill gaps in our understanding, and aid regional collaborative research efforts. Explore ways and means of facilitating exchange of scientists between laboratories and on research cruises.
3. Convene "hands-on" practical workshops with krill biologists (including students and established scientists) from PICES member countries to help them initiate and carry out krill research programs. Workshops could be convened before PICES meetings, or at other times as appropriate. A protocol for experimental work has already been published on the PICES website, http://www.pices.int/projects/Euphasiid/PICES%20Protocols%20COMPLETE.pdf.
4. Initiate euphausiid research programs in PICES member countries which will include sampling on a regular basis (biweekly-monthly) to determine seasonal cycles of spawning and growth, and incubations of live animals for measurement of brood size and molting rates.
5. Work with modelers to better parameterize euphausiids in the NEMURO and other models so as to explore their role in coastal and oceanic food chains.
6. Convene a krill workshop at the GLOBEC Open Science Meeting (May 2009).
7. Organize a Krill Symposium or a Topic Session at PICES XX in 2011, and submit a set of krill synthesis papers for a special issue of a scientific peer-reviewed journal.

Parent Committee

Biological Oceanography Committee (BIO)

Timetable

October 2007 – Proposal to establish a Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* (WG 23) submitted to BIO at the PICES Sixteenth Annual Meeting (PICES-2007) in Victoria, Canada.

- During 2007–2008, appoint members;
- Each member to work on compiling data available (with metadata);
- Chairman to prepare a "proposal" for how we will (a) fill gaps in our understanding, and (b) how to facilitate scientist exchange programs.

Year One – Starts with WG 23 holding its first meeting at PICES-2008 in Dalian, China.

- Discuss data/metadata. What kinds of data do we all have? Are there unpublished theses and other unpublished data available?
- Ratify a research plan that is designed to fill gaps in understanding;

- Discuss modeling efforts with the MODEL Task Team;
- Discuss ways and means of implementing scientific exchanges;
- Co-convene a krill workshop with GLOBEC at the GLOBEC Open Science Meeting in Victoria, Canada, in May 2009.

Year Two – Starts at PICES-2009 in Jeju, Korea.
- Convene a workshop to review status of research and modeling of krill dynamics.

Year Three – Starts at PICES-2010 in Portland, USA.
- Convene a workshop at the PICES Annual Meeting;
- Discuss results of research.

October 2011 – WG 23 term ends at PICES-2011 in Khabarovsk, Russia.
- Convene special Krill Symposium, or a Topic Session at PICES-2011 to include (if possible) the Antarctic krill community of scientists. This would follow the GLOBEC Open Science Meeting meeting by two years.

1.2 Outcomes of WG 23 beyond the Terms of Reference

1. All terms of reference were satisfied, with TOR #3 varying slightly from the original proposal. Although convening "hands-on" workshops on techniques of live euphausiid experimentation did not turn out to be feasible, the laboratory led by Dr. William (Bill) Peterson (the Peterson lab), located at the Hatfield Marine Science Center, NOAA-Fisheries, in Newport, Oregon, hosted scientists from Chile, China, Japan and Germany, and one member from this lab participated in several research cruises with Korean scientists in the Yellow Sea. These international collaborations included experiments on live euphausiids to measure molting and growth rates, egg production, feeding preferences and rates, and effects of hypoxia. Scientists from China and Korea also conducted live krill experiments in conjunction with their research cruises using the "Euphausiid Live Work Protocol" published to the PICES website by the Peterson lab in 2005.

2. The Peterson lab hosted and trained a Ph.D. student, Xiuning Du, from the Ocean University of China in Qingdao. She conducted experiments on feeding rates and preferences of *Euphausia pacifica* which comprised a substantial portion of her Ph.D. thesis. Xiuning Du was honored at PICES-2010 in Portland, Oregon, with the "Best Oral Presentation" award in a BIO-sponsored Topic Session.

3. Dr. Peterson spent two weeks in Qingdao, China, in December 2011 attending the Ph.D. defense of Ms. Xiuning Du and presenting seminars at each of the four oceanographic institutes in Qingdao. During that time, Dr. Peterson was appointed to an Adjunct Professorship at Ocean University of China by Prof. Quangxing Lu.

4. Dr. Peterson traveled to Qingdao in May 2012 for one week to collaborate with WG 23 Co-Chairman, Prof. Song Sun, on the preparation of this report.

5. Working Group member, Tracy Shaw (USA), participated in cruises to the Yellow Sea in August 2011, April 2012, and April 2013 with Dr. Se-Jong Ju's (WG 23 member from Korea) laboratory on the Korean research vessel R/V *Eardo*.

6. The Peterson lab hosted a Chilean Ph.D. student, Ramiro Riquelme-Bugueño, during the summer of 2011 after his lab in Concepción, Chile, was destroyed by a tsunami in February 2010. This collaboration explored the utility of using measurements of the euphausiid hepatopancreas as an indicator of physiological condition.

7. Dr. Peterson obtained funding for preliminary analysis of the population genetics structure of *Euphausia pacifica*. To compare individuals from a variety of geographic locations, *E. pacifica* specimens were obtained from WG 23 members in the Oyashio region of Japan (Yuji Okazaki), the Yellow Sea (Se-Jong Ju), the Bering Sea (Tracy Shaw as part of the BEST project), and Oregon (Peterson lab).

8. The successes of WG 23 inspired a proposal to establish a working group on zooplankton production led by Dr. Toru Kobari (Japan).

2 State of Knowledge of Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim

Below we provide excerpts from a proposal to the U.S. National Science Foundation that was funded in 2008. Many ideas and topics for discussion within WG 23 were taken in part from this proposal and it is included here to provide an overview of the state of our knowledge of *Euphausia pacifica* and *Thysanoessa* spp. in the North Pacific at the time the proposal was written.

2.1 U.S. GLOBEC Pan-Regional Synthesis — Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim

2.1.1 Introduction and Background

The U.S. GLOBEC program was initiated to develop a broader understanding of climate impacts on marine ecosystems. In this proposal we seek funds to synthesize knowledge of North Pacific krill through modeling and comparative studies across U.S. GLOBEC, Japan GLOBEC, China GLOBEC and related study regions. Within the GLOBEC Northeast Pacific (NEP) program, our past research addressed the three goals listed below:

- Quantify how physical features in the NEP and variability related to climate change impact zooplankton biomass, production, distribution, and the retention and loss of zooplankton from coastal regions, and how these in turn influence the distributions of higher trophic levels such as forage fish, salmon, and marine birds and mammals;
- Quantify the impacts of key coastal physical and biological processes on controlling juvenile salmon growth and survival in the coastal zone of the NEP;
- Compare the impacts of climate variability and change (such as ENSO cycles and PDO-related regime decadal variability) on similar marine animal populations (copepods, euphausiids and salmon) across the sub-regions of the NEP.

Within the goal of understanding climate impacts on euphausiids, we will follow two of the three research themes outlined in the U.S. GLOBEC Pan Regional Synthesis Program Solicitation:

- The response of krill populations at local and regional scales to basin- and global-scale change in climate forcing;
- Identify the processes controlling the population dynamics and recruitment of krill as a function of ecosystem type and ascertain how these processes would be affected by climate change, to be accomplished through comparing/ contrasting population responses from a number of different North Pacific ecosystems.

The U.S. GLOBEC NEP program identified krill as a target species because they are far less studied than copepods, yet they are among the most important links in coastal and oceanic food webs, transferring energy from primary and secondary producers to higher trophic level animals such as salmon, herring, sardines, mackerel, Pacific whiting, sablefish, many rockfish species, auklets, shearwaters and whales. Furthermore, GLOBEC highlighted the need for research that focused on krill because many aspects of their basic biology and ecology were not well understood. One species of euphausiid, *Euphausia*

pacifica, is of special interest because of its broad distribution throughout most of the North Pacific Ocean (see Figure 2.1.1). Across this range, it occupies a diversity of habitats, including cool upwelling regions off Mexico's Baja California, California, Oregon, Washington and British Columbia, the downwelling environment of the Gulf of Alaska, shelf-break/slope waters of the Bering Sea, oceanic regions across the North Pacific Current and sub-arctic Pacific in water north of ~ 40° N, and south through the western Pacific from Russia (Sea of Okhotsk) to China and Korea (Yellow Sea). In the western Pacific this species inhabits waters where temperatures range from sub-arctic (*e.g.*, the Oyashio and Bering Sea slope waters) to sub-tropical (the Kuroshio, and the East China and Yellow seas). There are few invertebrate species that occupy such a wide variety of marine ecosystems and such a wide range of latitudes. Thus, we ask, "What are the unique characteristics of the life history and ecology of this cosmopolitan euphausiid species that allow it not only to populate such a wide variety of ecosystems, but to become dominant among the plankton?"

2.1.2 Synthesis of Observations and Experiment

Because of our krill-centric U.S. GLOBEC-funded research, as well as research carried out by biological oceanographers in China, Korea, Japan, Russia, Canada, and the USA, a rapidly growing amount of information has become available on the phenology, seasonal cycles of abundance, feeding, reproduction, and growth rates of *E. pacifica*. Our aim is to determine unique aspects of its life history and adaptations that permit it not only to exist but to prosper in a wide variety of environments across the North Pacific. Comparative studies are needed for analysis of the adaptations which allow this species to prosper in so many different regions. Armed with this basic information we will be in a better position to learn how climate change may affect its population dynamics.

The comparisons will also include synthesis of data on the less-well studied genus *Thysanoessa*. *T. spinifera* is the other dominant *Thysanoessa* species in the California Current which, along with *E. pacifica*, makes up ~ 90% of the biomass of krill in the northern California Current (NCC) (Gómez-Gutiérrez *et al*., 2005). *T. spinifera* is a coastal species in the NCC but extends into offshore waters off northern and central California (Brinton, 1962), likely because of extensive offshore transport of coastal waters in cold mesoscale upwelling jets, filaments, and eddies. This species is the dominant euphausiid in the coastal Gulf of Alaska; however, in the Bering Sea *T. spinifera* is replaced by *T. raschii*, *T. inermis* and *T. longipes*. *T. raschii* and *T. longipes* continue to be dominant in the western Pacific where they achieve phenomenal biomass in the Sea of Okhotsk (*T. raschii* in shelf waters and *T. longipes* in deep water offshore).

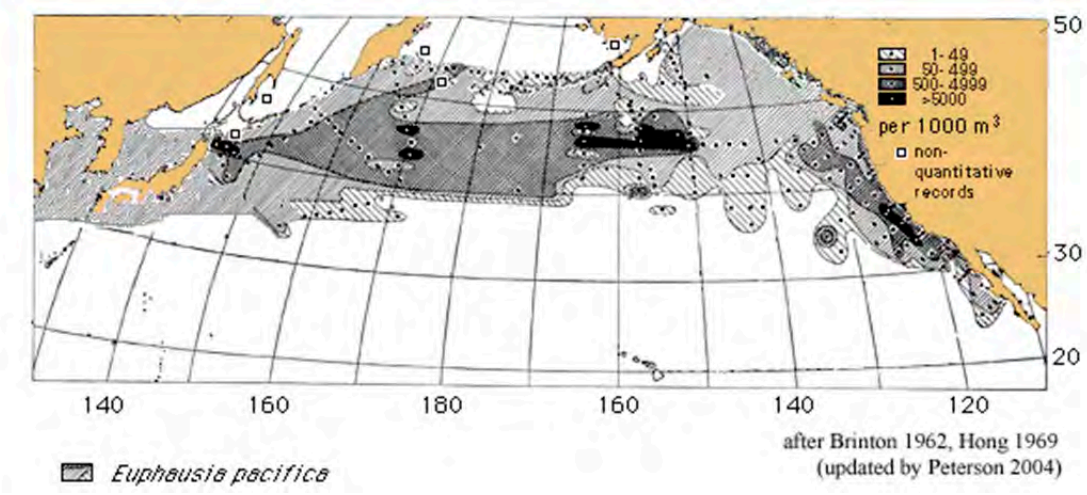

Fig. 2.1.1 Pan-Pacific distribution of *Euphausia pacifica*, redrawn from Brinton (1962) and updated to include the Far Eastern Marginal Seas.

We believe that this synthesis proposal to summarize the life history and ecology of these krill species has a high probability of success because we are personally acquainted with most of the krill researchers in the North Pacific. This has come about because of our 10 years of involvement in PICES (North Pacific Marine Science Organization) an international science coordinating body similar to ICES in the North Atlantic. We have been active in the Climate Change and Carrying Capacity (CCCC) program of PICES (Dr. Harold (Hal) Batchelder has been Co-Chairman of CCCC since 2001; Peterson chaired the Regional Experiments (REX) Task Team of CCCC from 1999–2006, has chaired workshops and special sessions on comparative ecology of krill at PICES Annual Meetings, and now chairs the newly established Working Group 23 on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim*). Also, a document on the PICES website (see http://www.pices.int/projects/Euphasiid/PICES%20Protocols%20COMPLETE.pdf) published in 2005 presents "Protocols for measuring molting rate and egg production of live euphausiids".

2.1.3 Synthesis through Modeling

Another strength of PICES is the ecosystem modeling work carried out chiefly by Japanese and U.S. scientists. Many scientists within PICES have contributed to the development of NEMURO (**N**orth Pacific **E**cosystem **M**odel for **U**nderstanding **R**egional **O**ceanography) and NEMURO.FISH (NEMURO **F**or **I**ncluding **S**aury and **H**erring) and to the application of NEMURO, EcoSim and ECOPATH models to the study of ecosystem dynamics in the North Pacific. PICES scientists would benefit greatly from a synthesis of the existing knowledge on *E. pacifica* and other euphausiids, including regional differences, so that the euphausiid component of these ecosystem models can be properly parameterized. Improvements to the models will result in tools that will allow us to investigate quantitatively the role of euphausiids in food chain dynamics and the potential impacts of climate variability and change on their population dynamics.

Modeling of krill can be multifaceted, including (1) local biophysically-coupled individual-based, Lagrangian models of krill to explore detailed interactions of life-history behavior and physiology with physical conditions and transports, and (2) Eulerian, coupled ecosystem-physical models based on NEMURO modified to include euphausiids and ROMS (or other physical models). The former type of modeling will continue work begun by Dr. Batchelder under a NOAA funded GLOBEC NEP synthesis project. He developed particle tracking code that links an Individual-Based Model (IBM) of euphausiid bioenergetics and behavior to velocity and temperature fields derived from Regional Ocean Modeling System (ROMS) simulations. Physical fields are derived from 10 km (NEP) and 3 km (CCS) ROMS models, but the population dynamics and tracking code was interfaced with other ROMS results. The initial focus was on coupled population dynamics-physical simulations in the Northern California Current in 2002 for which the best field observations were available for comparison. The model, named POPROMS, runs efficiently to advect individual organisms through the domain off Oregon and Northern California. We explored the interaction of ontogenetically determined diel vertical migration and alongshore and zonal water circulation, and specifically, we used coupled Forward-in-Time-Trajectory (FITT) and Backward-in-Time-Trajectory (BITT) simulations (Batchelder, 2006) to examine processes potentially responsible for aggregations of euphausiids along the shelf break (Ressler *et al.*, 2005). Simulations were done for 90-day periods spanning June, July and August 2000. We focused on BITT simulations since what we know from plankton surveys are the regions where individuals were captured, and what we wish to know is where the individuals were at earlier points in time and what conditions they experienced. Simulations have been completed for scenarios where individuals are fixed to certain depths (*e.g.*, 5, 35, and 95 m), and for simulations in which individuals undergo diel vertical migrations of various amplitudes (5–>35 m; 5–>95 m; 5–205 m). These different amplitude migrations are representative of the observed amplitudes of different life history stages of *E. pacifica*, the target organisms of this project. We have also done simulations where the amplitude of diel vertical migration is life-stage dependent and progression through the life history is temperature dependent.

The IBM has focused on including reasonably realistic biological dynamics in the POPROMS coupled model. To couple biological models with physical models we need to describe the vital rate processes of *E. pacifica*. Specifically, we need to parameterize the processes of respiration, growth, and development. To complete model closure, we need to parameterize survival and

reproduction; however, for the simulations we have done to date, we are considering the dynamics from egg to first juvenile (*e.g.*, the larval stages of *E. pacifica*), thus, we can ignore reproduction. Moreover, since survival rates are quite variable and difficult to estimate from observations, we ignore mortality effects. Respiration is parameterized as an allometric (individual weight dependent) function that includes a fixed cost and a variable cost related to consumption. Growth is allometric and depends primarily on food consumption, but also secondarily on environmental temperature. Development rate is stage-based and dependent on a nonlinear Belehradek function between temperature and stage duration (using data reported in Ross (1982) and Feinberg *et al.* (2006)). Since the earliest life stages—egg, nauplius and metanauplius—are non-feeding, we focus on only the feeding larval stages (Calyptopis-I to Furcilia-VII). We assume a Calyptopis-I of *E. pacifica* has an initial biomass of 3 μg C. Since both respiration and growth are food dependent, we need to specify the spatial distribution and concentration of food resources throughout the model domain, and through time. The physical simulation is not coupled with a lower trophic level ecosystem model, so instead we use the spatially mapped fields of chlorophyll estimated from the spring and summer GLOBEC SeaSoar surveys in 2002. We obtained the irregularly spaced SeaSoar Chl-*a* data from the U.S. GLOBEC data server and regridded the June and August surveys to a regular rectangular grid. We developed routines to interpolate Chl-*a* to an individual's location in space from the gridded fields. We assumed a linear interpolation in time between the two temporal three-dimensional maps of chlorophyll.

Individuals initialized to specific starting locations were examined for several specific cases: (1) fixed location, but dynamically evolving temperature and prey fields, (2) horizontal advection, with dynamically evolving temperature and prey fields, but individuals fixed to specific depth horizons (*e.g.*, 5, 35, 85 m, *etc.*), and (3) horizontal advection, with dynamically evolving temperature and prey fields, and vertical position controlled by stage (*e.g.*, temperature) dependent diel vertical migration (DVM). Simulations were run from June 1 to August 30. Since development and growth are primarily dependent on temperature and food concentration, respectively, we expected to find that there would be locations where growth was fast, but development was slow and *vice versa*. In upwelling regions, like the Oregon region studied here, nearshore, cold water regions have high food (slow development, fast growth), while offshore warm water regions have low food (fast development, slow growth). Realistically, the only places where *E. pacifica* are likely to survive are locations where a balance of growth and development is achieved. In Case 1 (fixed location) simulations, growth is best in nearshore regions and poorest in offshore regions. In Case 2 (horizontal, fixed depth) simulations, larval euphausiids that start on the shelf on June 1 are mostly advected off the shelf within 30 days, with the duration of shelf residence also partially controlled by the depth at which the individuals are fixed. When individuals are advected off the shelf and into generally low-food environments, weight of the individual begins to decrease as respiratory losses at high temperatures offshore exceed consumptive gains. In general, DVM (Case 3) moves animals between shallow depths during the night and deeper depths during the day, but this vertical movement alone was not sufficient to retain individuals on the shelf for more than about 30 days—eventually, most individuals ended up offshore, perhaps because of the influence of two large eddies off the shelf in the domain. Results of this research were shown at several scientific conferences or workshops.

The NEMURO model has become a *de facto* standard ecosystem model for pan-regional comparisons in the North Pacific (Batchelder and Kashiwai, 2007; Werner *et al.*, 2007). The base lower trophic level NEMURO model has 11 state variables: dissolved nitrate, ammonia, and silicate; small and large phytoplankton; small, large and predatory zooplankton; particulate silica and organic nitrogen; and dissolved organic nitrogen (Kishi *et al.*, 2007a,b). The base NEMURO model has been extended in various ways, depending on the specific application and scientific interests, including extension to include carbon biochemistry (Fujii *et al.*, 2007) and higher trophic levels, in particular to describe growth and population dynamics of saury and herring (Ito *et al.*, 2007; Megrey *et al.*, 2007b; Mukai, *et al.*, 2007; Rose *et al.*, 2007). NEMURO has been used to examine interdecadal variability (Aita *et al.*, 2007) and regional differences (Megrey *et al.*, 2007a). It has not been extended to model the dynamics and energetics of krill. That is a goal that this synthesis project will pursue, especially as a collaboration of Dr. Batchelder and Professor Michio Kishi (Tokyo University). Dr. Kishi, a member of PICES WG 23, is one of the originators of the NEMURO project and has expressed great interest in

working with us to develop a model that can represent krill. This is especially important given the recent emphasis on linking NEMURO to various fish species, as none of the three zooplankton state variables in the present version of NEMURO is parameterized in any way like krill would need to be. Addition of a krill state variable to NEMURO would not only enable prediction of krill dynamics in multiple Pacific regions, but would also significantly improve representation of processes linking plankton production to fish.

2.1.4 Synthesis of U.S. GLOBEC Observations: Copepod and Krill Observations off Oregon

Because of funding from U.S. GLOBEC, NOAA, and the Bonneville Power Administration, we have accumulated and compiled an extensive long-term data set on observations of ocean conditions in coastal waters of the Pacific Northwest, and on the nutrients, phytoplankton, copepods, krill, ichthyoplankton, sardines, anchovies and juvenile salmon that live within these waters. The data have come from three time series.

The Newport Time Series

The Newport time series was established in 1996 and is based on biweekly cruises off Newport, Oregon (44°40′N). Seven stations are currently sampled across the continental shelf and slope, at distances of 1, 3, 5, 10, 15, 20 and 25 nautical miles from shore in water depths ranging from 20 to 300 m. Sampling includes a CTD profile (Seabird 19+ with WetStar fluorometer and Seabird 43 oxygen sensor), Secchi disc depth, a surface sample for nutrients, phytoplankton species and chlorophyll, a vertical plankton net tow from 100 m to the surface (or from 5 m off the bottom to the surface in shallower waters) with a ½ m diameter 200 µm mesh net, and an oblique Bongo tow of the upper 20 m (60 cm diameter, 333 µm mesh net). Since 2001, most of these cruises have been at night so as to collect adult euphausiids. During the nighttime cruises, euphausiids from one side of the Bongo tow are used for live animal experiments – we incubate individual krill in 500 ml or 1 L jars, 30–60 individuals for molting rates and up to 20 females for brood size measurements. Animals are also returned to the shore laboratory as needed for other experiments on developmental rates, long-term variations in brood size and inter-brood periods, and grazing rates. Data on distribution and abundance of copepods, euphausiid eggs, larvae, juveniles, and adults from these cruises are supplemented by a wealth of historical data on hydrography, copepods and euphausiids from samples collected in 1969–1973, 1983, 1990–1992 (copepods and euphausiid eggs and larvae) and 1963–1967 (Smiles and Pearcy, 1971) and 1971–1972 (Gómez-Gutiérrez *et al*. 2005) for juveniles and adults.

The GLOBEC LTOP Time Series

We also sampled zooplankton and euphausiids at approximately 40 stations, ranging from 1–85 nautical miles from shore and water depths to ~4000 m along five transects from Newport south in February, April, July, September and November as part of the GLOBEC Long Term Observation Program (LTOP) cruises. Physical, chemical and chlorophyll data are available on line for each station (http://ltop.oce.orst.edu/~ctd/index.html). We also sampled zooplankton at approximately 100 stations during each of four GLOBEC "mesoscale" cruises (MESO) in June and August 2000 and 2002, and mapped oceanographic features and zooplankton from Newport south to Crescent City, to resolve finer-scale and feature-specific copepod and krill distribution and abundance associated with eddies, meanders, the upwelling jet and upwelling filaments. For both the LTOP and MESO cruises, zooplankton were sampled with a ½ m diameter (200 µm) net towed vertically from 100 m to the surface, and a 1 m^2 MOCNESS (333 µm) in depth-stratified tows from 500 m to the surface.

The Bonneville Time Series

The relevant feature of the Bonneville time series is that it includes zooplankton sampling, as described above, along transects perpendicular to the coast off Oregon (Cascade Head and Cape Meares) and off Washington (just south of the mouth of the Columbia River, Willapa Bay, Grays Harbor, Queets River and La Push). Thus (as with GLOBEC-LTOP time series), we are able to place the Newport time series within a spatial context.

2.1.5 Synthesis of Krill Ecology in Coastal Waters off Oregon and Washington

The Newport time series is now of sufficient length (16 contiguous years) that when coupled with the historical data sets from the 1960s and 1970s, the potential impacts of climate change on lower trophic level organisms (copepods and euphausiids) can be investigated. Moreover, we can compare our seasonal cycles of temperature-chlorophyll-copepods-euphausiids to cycles associated with the PDO, NPGO and ENSO. The observation that the PDO has cycled at a much higher frequency lately has provided us with a natural experiment that will allow us to infer mechanisms by which the ecosystem change might be related to PDO cycles; some of these are discussed for copepods in Hooff and Peterson (2006). Global warming appears to be accelerating (IPCC 4th AR), and to investigate how warming will impact ecosystems, we will need "baselines" (which we now have), based both on recent data (1996–present) and on data from the late 1960s and 1970s. From our recent work on North Pacific krill, we have established the following.

Krill biomass peaks in autumn as juvenile stages that were born during the July–August phytoplankton blooms during the summer upwelling season mature. These juveniles become the adults that may spawn as early as the following winter (if a February phytoplankton bloom occurs), but which will spawn during spring and summer blooms associated with coastal upwelling.

Stage-specific development times and developmental pathways were worked out in laboratory experiments in which individuals were raised from eggs and maintained in the laboratory for more than two years. Detailed information on developmental rates and progression through instars resulted from daily examination of larvae from egg to juvenile (Feinberg *et al*., 2006). These known-age animals were also used to calibrate the lipofuscin technique for *E. pacifica* which was subsequently used to age wild populations and specifically reproductive females (Harvey *et al*., 2010).

Egg production was further investigated by measuring brood size of females collected and incubated during cruises (Gómez-Gutiérrez *et al*., 2006, 2007). Potential differences in brood sizes and interbrood period (IBP) were investigated for two populations of *E. pacifica* (Oregon and Santa Barbara, California) and we found that brood size was the same but IBP was one day shorter for the Santa Barbara females, 4 *vs*. 5 days (Feinberg *et al*., 2007). We also compared the brood size of *E. pacifica* females from Japan, Puget Sound and Oregon and found that brood sizes were the same after correcting for female length (Gómez-Gutiérrez *et al*., 2006).

Growth. Euphausiids have a strong cohort age structure (Smiles and Pearcy, 1971; Brinton, 1976; Shaw and Peterson, unpublished data). We have shown from cohort data that growth rates estimated from cohort analysis are similar to growth rates estimated from incubations of animals collected during our cruises (Shaw *et al*., 2010).

Molting. Intermolt periods measured from molting rate incubations range from 2–20 days with a median of 8–10 days (Shaw *et al*., 2010). We have also staged animals in the molt cycle by examining development of setae in the uropods (following Dexter, 1981). We refined this work and have shown that one can estimate molting rates from preserved samples by staging animals and then using the proportion of individuals in pre-molt stage as an indicator of the animals that should molt within 48 hours (Jarvis *et al*., unpublished report on her work carried out as a summer intern).

Feeding. *E. pacifica* feeding rates on suspensions of *Rhodomonas salina* were determined at concentrations ranging from 50 to 800 µg L^{-1} (Sremba and Peterson, in prep.[1]). Animals could consume up to 30% of their body weight per day. Trials with foods of other sizes showed that they could feed on cells as small as 4.5 µm in diameter (*Isochrysis galbana*). Perhaps this is one adaptation that allows them to prosper not only in coastal waters but in oligotrophic oceanic waters of the North Pacific where cells are typically of this size. Analysis of the lipids in wild *E. pacifica* indicated the importance of diatoms in their diet, but a comparison to the lipids found in the seston also suggested a degree of selective feeding (Ju *et al*., 2006).

Cross-shelf distributions. *T. spinifera* is usually found only in shelf waters except in one year, 2002 – during that summer females were consistently found offshore of the continental shelf. *E. pacifica* is most abundant at and beyond the shelf break; however, it

[1] Remains unpublished.

is carried into the nearshore upwelling zone with the deep upwelled water in the same manner as described by Peterson *et al.* (1979) for *Calanus marshallae*. Shoreward transport of adults during the July–August peak period of upwelling and phytoplankton blooms often results in spawning and may lead to egg concentrations in excess of 1000 eggs m^{-3}. Larvae are subsequently found at greater distances from shore with ontogeny (Feinberg and Peterson, 2003 and unpublished data). Predation by large scyphomedusae may result in high mortality of euphausiid eggs in this nearshore zone (Suchman *et al*., 2008).

Diel vertical migration. DVM was investigated from analysis of more than 300 samples from 40 MOCNESS tows. In shelf waters, eggs are found only near the surface whereas in deep off-shelf waters, eggs are usually found at depths > 200 m. The first developmental stage to perform DMVs is Furcilia III (Vance, unpublished). This is also the stage where all swimming appendages first become well developed. In oceanic waters, adults migrate from depths of 200–300 m; in shelf waters it would appear that adults reside on or very near the sea floor during the day (Ressler *et al*., 2005) but migrate to the surface at night.

Ciliate–euphausiid interactions. We discovered that a ciliate, *Gymnodinioides pacifica*, can invade the bodies of *E. pacifica* and *T. spinifera*, consume the internal organs and, through rapid cell division, cause the adults to rupture (Gómez-Gutiérrez *et al*., 2003). Other species of ciliates consume the organic matter that remains inside euphausiid molts (Landers *et al*., 2006), suggesting that the idea of Jerde and Lasker (1966) that euphausiid molts are an important source of organic matter to the deep sea is unlikely.

2.1.6 Synthesis and Resource Assessment and Management

A final aspect of krill ecology that needs investigation is the degree to which euphausiids can be harvested commercially. Nicol and Endo (1999) provide a fascinating review of this issue. *E. pacifica* is currently harvested off the northeast coast of Honshu (Japan) and in the Strait of Georgia (Canada). Presently, harvest of *E. pacifica* in the California Current is prohibited (http://www.pcouncil.org/wp-content/uploads/CPS_Am12_Krill_DraftEA.pdf). Given the cap on harvesting *E. superba* in the Antarctic, we can expect continued pressure from commercial fishers to increase harvest of North Pacific krill populations. Our synthesis activities will provide the information needed to conduct a formal stock assessment, as required for nearly all managed fisheries.

2.1.7 Proposed Pan-Pacific Research

Through synthesis of our own data as described above, and through synthesis activities carried out in collaboration with our PICES colleagues, one could evaluate and publish on a set of basic research questions such as those listed below. However, not all topics could be investigated during the life of PICES WG 23 but are presented here as ideas for future research:

- What are the seasonal variations in distribution, abundance, growth rates and brood sizes in krill populations, and how do they vary regionally around the Pacific Rim?
- Are growth rates and brood sizes related to seasonal cycles of primary production?
- How do populations in the eastern and western Pacific respond to ENSO and PDO cycles?
- How are individuals of the same species (*Euphausia pacifica*) adapted to survive year-around in the very warm water regions of, for example, the Yellow Sea and East China Sea? What mechanisms enable individuals to survive the long winters in northern regions, *e.g*., the Gulf of Alaska, Sea of Okhotsk and northern California Current?
- What interactions between physical transport and life-stage dependent dynamics control the local scale distributions of krill and are similar interactions important at regional and basin-scales around the Pacific?

Synthesis which focuses on a single species, *E. pacifica*, provides a common starting point for international exchanges and partnerships, largely because of this species' broad distribution. Scientists from PICES member countries have information and experience to share, and all would benefit from an increased understanding of this species. Moreover, synthesis work proposed here will further foster the exchange of ideas and will promote long-term collaborations among a culturally diverse set of established research scientists as well as graduate students and young investigators from the PICES member countries. *Thysanoessa* spp. will also be investigated; however, the biology and ecology of

this genus is at present far less well known than for *E. pacifica*; thus, we focus our efforts on the latter species.

Objectives

Data and metadata

We have already begun to obtain copies of all published research papers on *E. pacifica* and the three *Thysanoessa* species as an activity under PICES WG 23. For papers, monographs, and theses written in languages other than English, the abstracts, figure captions and table legends will be translated into Japanese (by Dr. Michio Kishi), Chinese (by Dr. Hongsheng Bi), and Korean (by Dr. Young-Shil Kang). We are working now to identify Russian translators of similar documents. Research results that are deemed critical but which are unavailable in peer-reviewed journals (theses, technical reports, cruise reports) will be translated fully then scanned so that an electronic file is created. All papers will reside on our server as well as on the PICES server to assure broad availability to all PICES and krill scientists worldwide. This activity will constitute one of our legacy products.

State of our knowledge

One of our key synthesis activities was devoted to distinguishing what is known from what is not known. Thus, published and unpublished work (*e.g.*, theses, technical reports, *etc*.) was identified and reviewed by WG 23 to pinpoint gaps in our understanding of krill ecology and population dynamics. Working Group members summarized what they believe to be known on "key attributes of krill life history and ecology" that pertain to *E. pacifica* and *Thysanoessa* spp. in their local/ regional waters.

Collaborative papers

This activity would include papers written by members of WG 23. Where possible, within national constraints, the data discussed in each paper will become part of the krill database, and thus a legacy product. In some cases, scientists from several member countries would collaborate on joint papers whereby each author would analyze his/her own data following the same techniques and using a common set of illustrations to facilitate comparisons. A recent paper by Heath *et al*. (2007) is a good example of a collaborative paper. Potential topics which may be covered in our Collaborative Papers and Monographs include the following:

- Biomass and seasonal cycles, where possible, of abundance of eggs, larvae, juveniles and adults of *E. pacifica* and *T. spinifera* within the GLOBEC–Northeast Pacific Region and in the western Pacific.
- Parameters of population dynamics and variations along latitudinal gradients, pan-Pacific:
  - Spawning and recruitment,
  - Age structure, sex ratios,
  - Eggs and larval abundances; survivorship and mortality schedules where possible,
  - Growth estimated from cohorts *vs*. growth estimated from direct measurements of growth from molting rate determinations,
  - Brood size and interbrood periods.
- Comparative life history of *E. pacifica* in coastal waters around the Pacific Rim. Here, one would discuss differences in life history strategies such as:
  - over-summering in the Yellow Sea (where surface temperatures exceed 25°C);
  - over-wintering off Oregon and in the Gulf of Alaska (when there is no primary production for at least three months);
  - shrinking as a strategy for reducing metabolic rates;
  - spawning seasons in relation to seasonal cycles of phytoplankton biomass and production;
  - developmental pathways/instars;
  - seasonal cycles of abundance, biomass and age structure in relation to seasonal cycles of temperature and phytoplankton production.
- Cross-shelf distributions of eggs/larvae/ juveniles/ adults to look at population maintenance strategies, cross-shelf transport, and hot spots. Data are available from Oregon, Canada and Alaska GLOBEC regions, and from monitoring programs off Hokkaido (A-Line) and Honshu, Japan (PM Line).
- Vertical distribution and diel vertical migrations of developmental stages.
- The use of one model in several places (NEMURO) and different models in different places (IBMs); the use of ECOPATH for the California Current (developed by Dr. Thomas Wainwright at NOAA-Fisheries, Newport).
- How will climate change affect krill populations around the Pacific Rim? We have a number of thoughts on this for euphausiids in the California Current, and discuss them later in this proposal.

This topic will also be treated by the PICES WG 23 members since it is likely that large-scale climate forcing will express itself regionally in fundamentally different ways.

Convene symposia

Drs. So Kawaguchi (CSIRO, Tasmania) and Bill Peterson (NMFS, U.S.) convened a workshop on "*Krill research: Current status and its future*" at the 4th International Zooplankton Production Symposium in Hiroshima, Japan, in May 2007. This workshop accommodated 42 contributions (18 oral presentations and 24 posters) and hosted more than 100 scientists, and resulted in the preparation of a Special Issue of Deep-Sea Research II that was subsequently published (Vol. 57, Issues 7–8) in early 2010. The overwhelming success of this venture led to recommendations by attendees that we convene another krill workshop which was planned to coincide with the final GLOBEC Open Science Meeting, held in June 2009 in Victoria, Canada. We had hoped to convene another krill worskhop at PICES-2011, but it was decided that this was too soon after the one in Victoria.

2.1.8 Topics and References on the Ecology of *Euphausia pacifica*

The references listed here illustrate the state of our knowledge of the ecology of *Euphausia pacifica* at the time this proposal was written. Publication dates of these references are through 2007.

1. Distribution

Brinton (1962), Pearcy (1976), Simard and Mackas (1989), Nishikawa *et al*. (1995), Taki *et al*. (1996, in Japanese), Brinton and Townsend (2003), Iguchi (2004), Ressler *et al*. (2005)

2. Seasonal cycles of biomass/abundance, spawning and recruitment

California: Brinton (1976, and many publications in CalCOFI Reports), Marinovic *et al*. (2002), Brinton and Townsend (2003), Abraham and Sydeman (2004), Linacre (2004), Croll *et al.* (2005), Dorman *et al*. (2005)

Oregon/Washington: Hebard (1966), Laurs (1967), Smiles and Pearcy (1971), Pearcy (1976), Peterson and Miller (1977), Feinberg and Peterson (2003), Gómez-Gutiérrez *et al*. (2005, 2007)

Vancouver Island: Mackas *et al*. (1997), Tanasichuk (1998a,b, 1999 and 2002)

Inland waters of Washington and British Columbia: Cooney (1971), Hulsizer (1971), Heath (1977), Ross *et al*. (1982), Bollens *et al.* (1992), Kunze *et al.* (2006)

Gulf of Alaska: Coyle-GLOBEC LTOP data; Cooney *et al*. (2001), Pinchuk and Hopcroft (2006, 2007)

Chinese waters: Cai (1986, in Chinese), Suh *et al*. (1993), Yoon *et al*. (2000), Wang *et al*. (2003, in Chinese), Xu and Li (2005)

Japanese coastal waters: Nemoto (1957), Iguchi *et al*. (1993, in Japanese), Taki *et al*. (1996, in Japanese), Taki and Ogishima (1997, in Japanese), Taki (2004)

Korean coastal waters: Hong (1969), Rebstock and Kang (2003)

Russian waters: Gorbatenko *et al*. (2006), Gorbatenko and Kiyashko (2007)

3. Developmental rates and developmental pathways (stages, instars)

Boden (1950), Ross (1981), Knight (1984), Suh *et al*. (1993), Iguchi and Ikeda (1994), Rumsey and Franks (1999), Feinberg *et al*. (2006), Pinchuk and Hopcroft (2006)

4. Egg production, brood sizes and interbrood period

Ross *et al*. (1982), Iguchi and Ikeda (1994), Tanasichuk (1998a, b), Gómez-Gutiérrez (2002), Liu and Sun (2002, in Chinese), Pinchuk and Hopcroft (2006), Gómez-Gutiérrez *et al*. (2006, 2007), Feinberg *et al*. (2007)

5. Growth and age structure of cohorts

Lasker (1966), Smiles and Pearcy (1971), Brinton (1976), Bollens *et al*. (1992), Iguchi *et al*. (1993, in Japanese), Taki and Ogishima (1997, in Japanese), Tanasichuk (1998a, b), Taki (2004)

6. Molting rates/growth rates in incubations

Lasker (1964), Jerde and Lasker (1966), Dexter (1981), Bollens *et al.* (1992), Iguchi and Ikeda (1995, 1999), Marinovic and Mangel (1999), Pinchuk and Hopcroft (2007)

7. Feeding rates and role as grazers

Lasker (1966), Parsons *et al*. (1967), Ohman (1984), Suh *et al*. (1991), Dilling *et al*. (1998), Passow and

Alldredge (1999), Nakagawa *et al*. (2001, 2003, 2004) Bargu *et al*. (2006)

8. Cross-shelf differences in larval abundance

Feinberg and Peterson (2003), Lu *et al*. (2003), Gómez-Gutiérrez *et al*. (2005)

9. Diel vertical migration

Brinton (1962, 1967), Youngbluth (1976), Bollens *et al*. (1992), Iguchi *et al*. (1993, in Japanese), Iguchi (1995, in Japanese), Taki *et al*. (1996, in Japanese), Rumsey and Franks (1999), Nakagawa *et al*. (2003), Endo and Yamano (2006), Kunze *et al*. (2006)

10. Swarming

Terazaki (1980), Endo (1984), Odate (1991, in Japanese), Kotori (1995), Nishikawa *et al*. (1995)

2.2 Ongoing Research Relevant to WG 23 Activities

A large number of research programs are in place around the Pacific Rim that continue to sample krill on a routine basis and/or conduct experiments with live krill. These are summarized briefly here to familiarize readers with the breadth of ongoing research on North Pacific krill. PICES scientists, especially members of WG 23, are uniquely capable of increasing our understanding of euphausiids because many oceanographic stations and monitoring lines have been, and continue to be, routinely sampled for hydrography and zooplankton. The experimental protocol for live euphausiid experiments written by the Peterson lab and published on the PICES website in 2005 (http://www.pices.int/projects/Euphasiid/euphasiid.aspx) provide PICES scientists with the information they need to collect living animals and measure brood sizes, molting, and growth rates as part of their existing research programs.

a. IMECOCAL, since 1997, off northern Baja California, Mexico, (Lavaniegos and others, Mexico),
b. CalCOFI, since 1950 (Ohman and others, Scripps),
c. Monterey Bay and CalCOFI Line 67 (Marinovic),
d. Gulf of the Farallones (field sampling of krill using nets and acoustics, plus sampling of krill in seabird stomachs (Sydeman),
e. Bodega Bay Line (Morgan),
f. Trinidad Head Hydrographic Line (Bjorkstedt),
g. Newport Line (since 1996 for eggs and larvae; since 2001, all stages, eggs through adults, at night) (Peterson),
h. Spatial surveys of eggs and larvae (Newport north to the tip of Washington State), June and September (Peterson),
i. Canada. Quarterly surveys off Vancouver Island shelf (Mackas),
j. Canada. Barkley Sound. Monthly surveys since 1992 (Tanasichuk),
k. Gulf of Alaska. GLOBEC LTOP data along Seward Line since 1998; continuing with North Pacific Research Board funding (Hopcroft),
l. Bering Sea. Multi-year surveys by NOAA (Napp) and others (Coyle); three-year study funded by NSF/BEST program (Lessard),
m. Russia. Routine sampling in Sea of Okhotsk, some in collaboration with Japan,
n. Japan. A-Line and PH Line off Hokkaido and Honshu (Yamazaki, Hokkaido University, Hakodate and Okazaki, Japanese National Fisheries Research Institute, Yokohama),
o. Korea. Bimonthly CTD and plankton sampling around all sides of the Korean peninsula (Kang and others)
p. China. Monitoring of ocean conditions in the Yellow Sea and East China Sea (Song Sun, IOCAS, Qingdao) and Yellow Sea Fisheries Research Institute (Shanghai).
q. Continuous Plankton Recorder (CPR) sampling: the north–south transect (between the west coast of North America and Alaska) is towed about six times per year and the east–west transect (between North America and Japan) is towed three times per year (Sir Alister Hardy Foundation for Ocean Science).

3 Country Reports

Summary reports from each PICES member country, including past and ongoing sampling programs, are presented below.

3.1 Canada

Canadian research on euphausiids not only includes many activities in the Northeast Pacific, but projects in the Northwest Atlantic, the Gulf of St. Lawrence and the St. Lawrence Estuary as well. In this report we detail only the Pacific efforts, but provide brief summaries and citations for the east coast work. On both coasts, the primary recent research topics have been interannual variability (temporal monitoring), spatial distribution (sites and mechanisms for formation of local aggregation), and development of bioacoustic and net tow sampling methodologies.

3.1.1 Time Series of Abundance, Biomass, and Species/Size/Age Composition

Vancouver Island continental shelf/slope

Interannual variability of euphausiid populations along the British Columbia continental margin is assessed as part of an ongoing 30+ year overall zooplankton monitoring program. Most sampling has been done using vertical net tows with black bongo nets fitted with TSK flow meter and 0.23 mm mesh). Depth ranges for the tows are near-bottom to surface on the continental shelf, and 250 m to surface at deeper offshore locations. Sampling is done both day and night, but abundance and biomass estimates from daytime samples include an estimated correction factor (~10×) for daylight net avoidance by adult and late juvenile euphausiids. Survey timing and number varies somewhat from year to year, but usually includes two major bio-oceanographic surveys in spring (May) and late summer (August–early September), plus additional sampling in February, June and September (Line P surveys) and mid-summer and autumn (done as part of juvenile fish surveys by DFO (Department of Fisheries and Oceans). The two dominant euphausiid taxa in this region (like elsewhere along the Pacific coast) are *Euphausia pacifica* and *Thysanoessa spinifera*. *T. inspinata* and *T. longipes* are often present and moderately abundant in samples from more offshore and northerly parts of the region. We normally report and analyze interannual variability of zooplankton as time series of log-scale annual biomass anomalies calculated relative to estimates of their long-term average seasonal cycles. Interannual variability of the euphausiids is high and also strongly coherent alongshore. Previously published local and coast-wide analyses include Mackas *et al*. (2001, 2004, and 2006). The Vancouver Island data are updated annually in DFO "State of the North Pacific" reports (*e.g.*, Irvine and Crawford, 2012). Figure 3.1.1 shows the most recent of these updates.

Barkley Sound

Barkley Sound is a sheltered but relatively deep water embayment located on the outer coast of Vancouver Island. Time series sampling targeting euphausiids has been done here since 1991 (although the future of this program is uncertain due to the recent retirement of project leader Ron Tanasichuk). Four standard sites have been sampled, nine times annually from 1991–1994, and five surveys per year (in January, March, June, August and October) subsequently. All sampling was done at night using bongo nets (0.33 mm mesh) towed obliquely from 10 m above the bottom to the surface. Samples were counted with very good size resolution (*e.g.*, Fig. 3.1.2) and have been used to estimate both growth and mortality rates of *E. pacifica* and *T. spinifera* (Tanasichuk, 1998a,b).

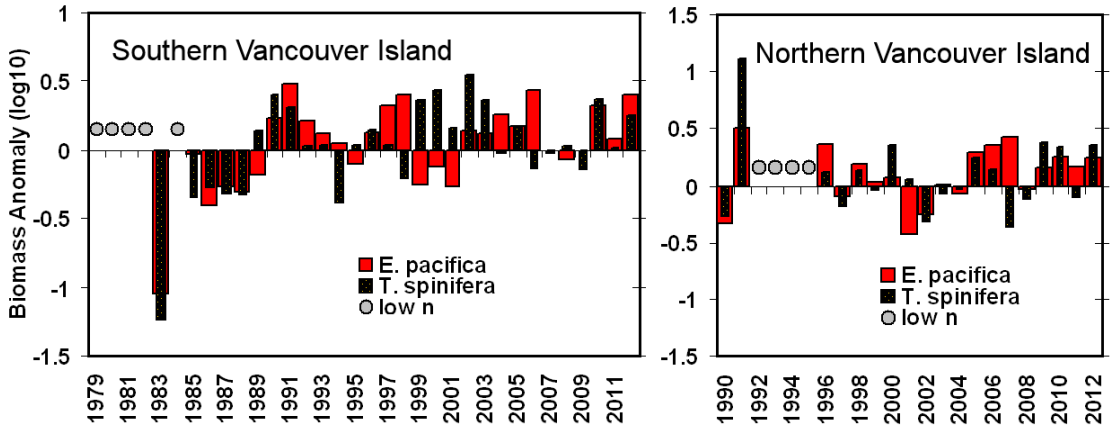

Fig 3.1.1 Time series of annual anomalies of *Euphausia pacifica* and *Thysanoessa spinifera* off Vancouver Island (from DFO Can. Sci. Advis. Sec. Res. Doc. 2012/072).

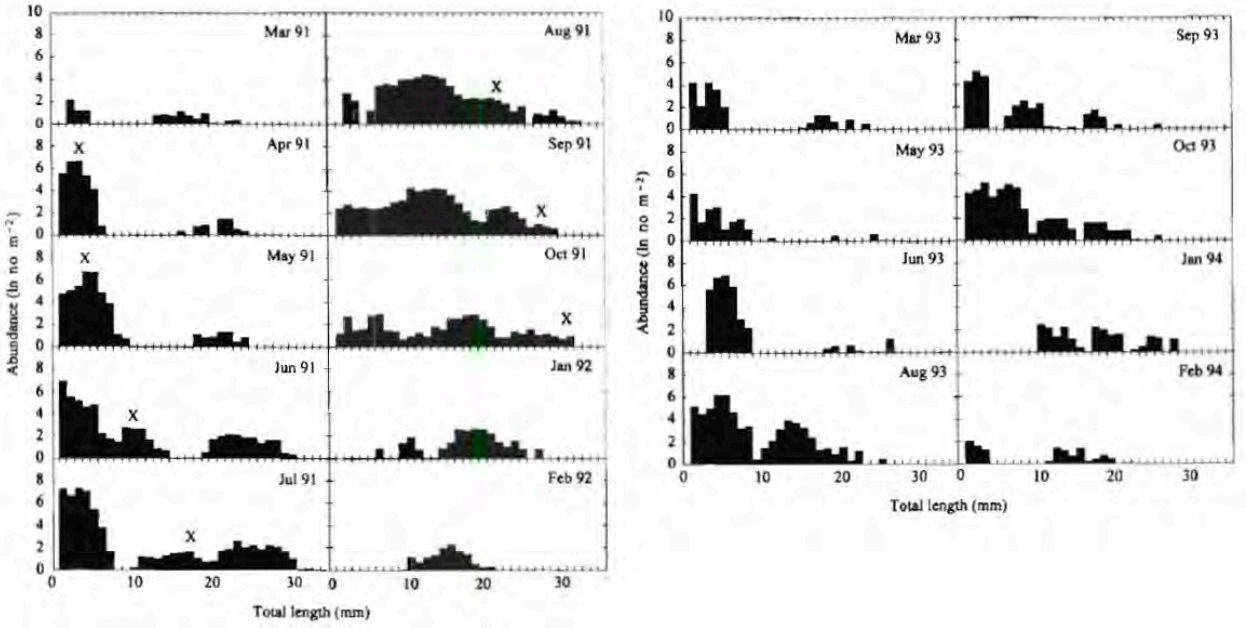

Fig 3.1.2 Seasonal and interannual variations in size and abundance of *T. spinifera* in Barkley Sound (from Tanasichuk, 1998b).

The early years of the Barkley Sound project benefited from a collaboration with University of Victoria graduate student Patricia Summers which produced the first egg-adult rearing of *T. spinifera*, and descriptions/drawings of all its larval stages (Summers, 1993). Recent analyses of the Barkley Sound data (*e.g.*, Tanasichuk and Routledge (2011) and annual DFO State of the Ocean reports) have focused on the importance of euphausiids to juvenile and adult fish, and their potential for predicting variations in fish recruitment.

Strait of Georgia

Despite the ecological importance of the Strait of Georgia, and the long history of scientific study by university and government researchers, there has been no consistent or sustained monitoring program for zooplankton (including euphausiids) in this region. However, there have been several high quality but shorter duration sampling programs. From this earlier work (*e.g.*, Heath 1977; Fulton *et al.*, 1982; Romaine *et al.*, 1995, 2002) we knew a lot

about species composition (strongly dominated by *E. pacifica*, but also including several *Thysanoessa* species), average biomass concentrations (high, but even higher in Malaspina Strait and Jervis Inlet, which support a small commercial harvest), within-Strait spatial distribution, seasonality of growth and reproduction, relative magnitudes of the fishery harvest *vs*. average levels and natural seasonal changes in population size (the fishery accounts for a very small fraction of total mortality). However, we knew relatively little about interannual and decadal variability and trends. In an effort to understand long-term changes in the Strait's food web, DFO recently compiled many of the data from earlier net tow sampling into a single database which is now available for various analyses. Two of these analyses (by Li *et al*. (in press) for nearshore locations around the periphery of the Strait, and Mackas *et al*. (in press) for mid-Strait deep water locations) have been completed and will soon be published. Both studies found high average biomass of euphausiids during most of the 1990s, but also very low population size during parts of the last decade (2000s). Fortunately, this decline seems to have ended (and reversed) after 2007.

Saanich Inlet and the VENUS undersea observatory system

Many euphausiid species are strong diel vertical migrators. Several of the pioneering studies of the extent and environmental cues for their vertical migration were done in Saanich Inlet (*e.g.*, Bary *et al*., 1962; Boden and Kampa, 1965). This tradition continues.

Extensive arrays of instruments connected to shore by a network of data and power cables are a relatively new tool and approach for ocean monitoring. Although cabled "undersea observatories" typically sample only a moderate number of fixed locations, they can do so for long time periods and at very high temporal resolution. This makes them especially useful for study of intermittent events (such as deep water renewal in coastal estuaries) and also for detailed study of changes in ~periodic phenomena such as the diel vertical migration of euphausiids.

The VENUS network (http://venus.uvic.ca/) includes several upward-looking high-frequency echo sounders. The Saanich Inlet node is the oldest of these and has provided very detailed records of the diel vertical migration of euphausiids (mostly *E. pacifica*) since June 2008 (Fig. 3.1.3). Sato *et al*. (2013) have analyzed this time series. They found that although timing of upward and downward migration approximately tracks seasonal changes in the timing of sunrise and sunset, the upward migration is slightly but significantly earlier and the downward migration later when daylight duration is longer.

East coast of Canada

A broad net-tow-based monitoring of zooplankton has been in place since 1999 in various east coast regions of Canada (part of the DFO Atlantic Zonal Monitoring Program, http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html). This includes euphausiids, but does not specifically target them in terms of sampling methodologies. However, there has been additional research using acoustic and optical sampling methods, especially at locations in the St. Lawrence Estuary (where euphausiid abundance and distribution are of great interest and importance to the growing industry of whale watching tourism; *e.g.*, Simard and Lavoie, 1999; Cotté and Simard, 2005) and in deep basins on the Nova Scotia shelf (where populations of *Thysanoessa inermis* and *Meganyctiphanes norvegica* provide forage for resident fish, *e.g.*, Herman *et al*., 1993; Cochrane *et al*., 2000).

3.1.2 Bioacoustic Sampling and Analysis

Because euphausiid spatial distributions are extremely patchy (see next section), bioacoustics sampling is often very useful to resolve and understand their spatial pattern. At various times during the past 30 years, there has been considerable Canadian developmental work on high frequency acoustic sampling and data analysis methods. For the Atlantic coast of Canada, references in the previous section are a good starting point, but see also Simard and Sourriseau (2009) for an examination of diel changes in target strength due to changes in body orientation and how these are affected by strobe-lights mounted on the nets used to obtain sea-truth samples. On the west coast, recent work includes a cross-taxa comparison of euphausiid, fish, and siphonophore target strengths at different acoustic frequencies (Trevorrow *et al*., 2005) and development of geostatistical methods for analysis of acoustic data (Romaine *et al*., 1995, 2002).

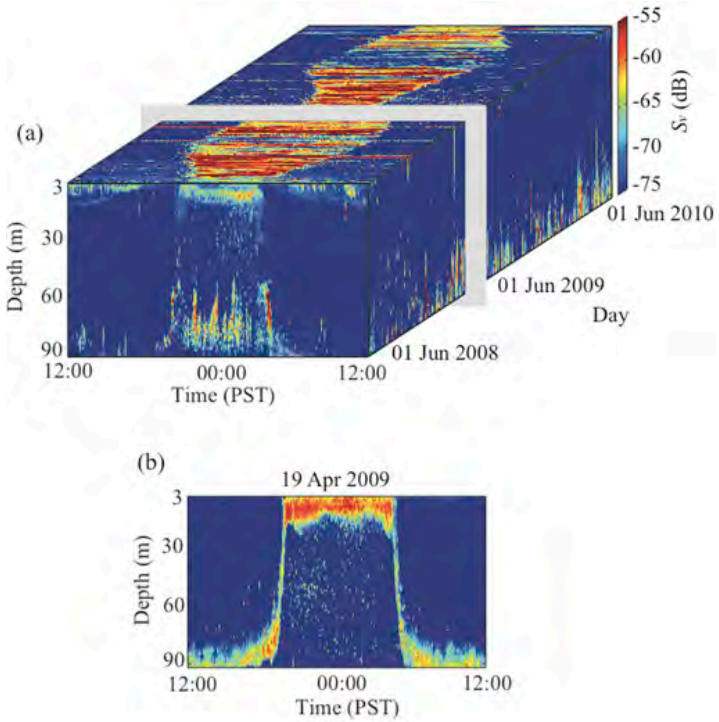

Fig 3.1.3 Seasonal and interannual modulation of euphausiid vertical migration timing and population density in Saanich Inlet (from Sato *et al*., 2013).

3.1.3 Spatial Distribution and Krill Aggregation Mechanisms

Research on spatial aggregation (where, when and why euphausiids form dense patches) has been the dominant theme of much recent Canadian euphausiid research. This work was pioneered on both Canadian coasts by Yvan Simard (*e.g*., Simard *et al*., 1986; Simard and Mackas, 1989), and he continues to be very active in the Gulf of St. Lawrence and St. Lawrence Estuary (*e.g*., Simard and Lavoie, 1999). Recent west coast work by others on three inter-related topics is summarized below.

Highest abundance along the continental shelf break and margins of banks or other steep slopes

We now have conclusive evidence from a wide variety of locations (*e.g*., Mackas *et al*., 1997; Romaine *et al*., 2002; Lu *et al*., 2003) that euphausiids and their predators aggregate along bathymetric "edges". These include the continental shelf break, the sides of submarine canyons, the margins of mid-shelf banks and basins, and the sides and sills of fjords. At these locations, euphausiid aggregations reform daily and rather quickly at the daytime depth of the euphausiid scattering layer, so almost certainly involve a "fast" behavioral mechanism rather than being primarily linked to "slow" population growth. While it is also likely that krill aggregation behavior has evolved to place aggregations (on average) in locations where growth is likely to be good, many of the sites of dense aggregations are prime feeding grounds for finfish, baleen whales, and other euphausiid predators, leading sometimes to elevated local mortality rates.

We also now know that the densest subsurface aggregations occur where and when advective transport at scattering layer depth is strongly convergent toward a sloping seabed (Fig. 3.1.4). Depending on location, this convergence can be driven by wind, meandering alongshore currents, or tides.

Spatial separation of adult and larval euphausiid life stages

Many years ago, Brinton and Wylie (1976) made the interesting observation that abundance of adult and larval life stages of euphausiids is negatively correlated in CalCOFI samples. At first glance, this seems odd given that much of the total adult (spawning) population is at any given time within a

fairly local aggregation, and adult aggregations at specific locations are often either persistent or recurrent. But in evolutionary terms such a relationship is also adaptive because it reduces risk of cannibalism of juveniles by adults. Lu *et al.* (2003) explored this question in the Vancouver Island continental margin environment and found that adults and juveniles are indeed often separated in a cross-shore direction by small, but ecologically significant, distances (order 10 km) (Fig. 3.1.5).

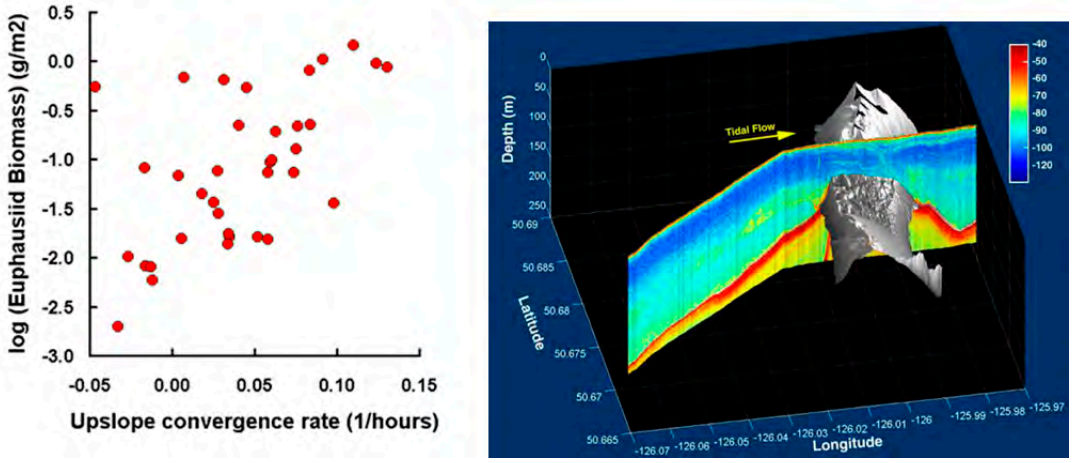

Fig. 3.1.4 Aggregation of euphausiids at bathymetric edges. Left panel (from Mackas *et al.*, 1997) compares local concentrations around the margin of Nitinat Canyon with local rate of convergence of horizontal flow. Right panel (courtesy M. Benfield) shows aggregation on the tidal-upstream side of the Knight Inlet sill, where flow direction and aggregation site reverse at tidal periodicity.

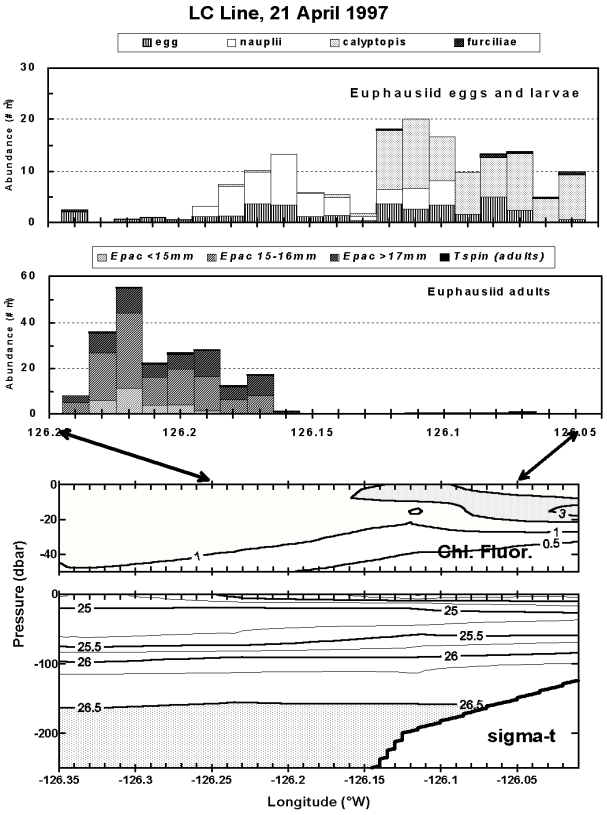

Fig. 3.1.5 Cross-shore separation of adult and juvenile euphausiid life stages (from Lu *et al.*, 2003).

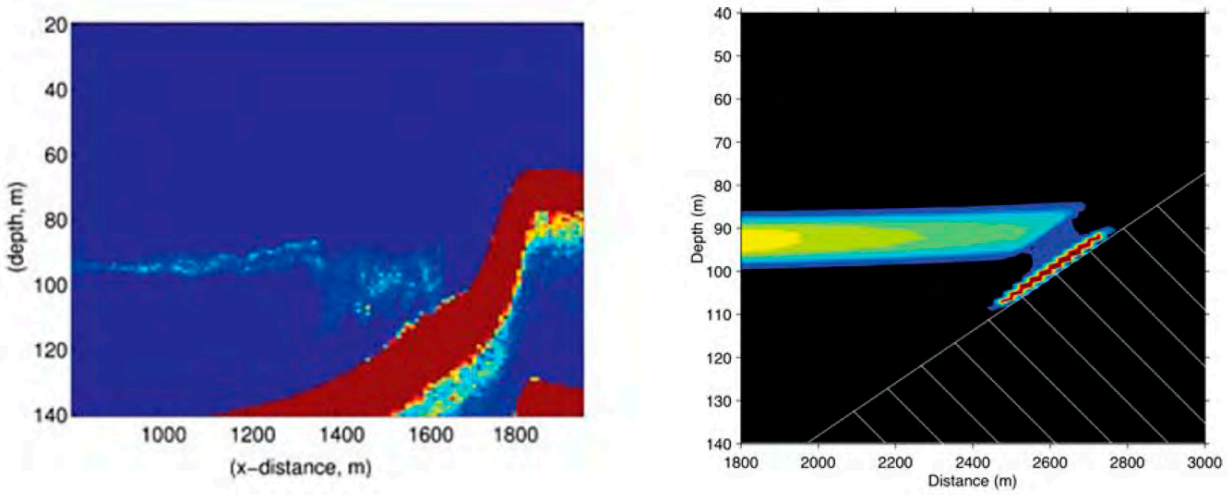

Fig 3.1.6 Observations (left) and model output (right) of intensification plus downward displacement of the euphausiid scattering layer (from Ianson *et al.*, 2011). Tidal flow is from left to right. To reproduce the downward displacement, euphausiids must swim downward when they encounter shear/turbulence in the bottom boundary layer.

Lu *et al.* (2003) concluded that the primary mechanism responsible for this separation of larvae and adults is the difference in daily cross-shore Ekman transport between larval stages that always inhabit the surface layer *vs*. adults that inhabit a deep (and counter-flow) layer for many hours of each day. Depending on local upwelling conditions (the data shown in Figure 3.1.5 are from downwelling conditions), larvae are displaced either seaward or shoreward from their parents.

Mechanism of aggregation by late juvenile and adult euphausiids

This is and remains a topic of active debate and enquiry. Simard and his colleagues interpret from observation in the St. Lawrence Estuary that the primary causal mechanism is light–depth maintenance against vertical displacement by tidal (or other) vertical displacements. However, our recent data from Knight Inlet (Fig. 3.1.4 and Ianson *et al*., 2011) strongly support an additional or alternative mechanism. The key observation (left panel in Fig. 3.1.6) is that the core aggregation gets deeper by about 10 m as it approaches the bathymetric barrier.

Model experiments (Ianson *et al*., 2011) show this downward movement is reproduced only if the euphausiids swim downward across light and depth contours. It does not happen if they are drifting passively with the tidal flow (in which case they are carried upward by the convergent flow) or if they are maintaining a preferred light depth (in which case the scattering layer intensifies less strongly and maintains a constant depth).

3.2 Japan

There are research projects that include krill studies at the following institutions in Japan: Tohoku National Fisheries Research Institute (2006–2011), National Research Institute of Far Seas Fisheries, The Institute of Cetacean Research, Tohoku University, and Hokkaido University. Recent research has taken place predominantly in the subarctic region of the western North Pacific. Target species of euphausiids are *Euphausia pacifica* and *Thysanoessa* spp. Research interests focus mainly on distribution and abundance. Projects are generally conducted by small groups or individuals at each institute as a component of a larger research program.

3.2.1 The ODATE Collection

The ODATE collection comprises more than 20,000 zooplankton samples (formalin preserved) which are archived at the Tohoku National Fisheries Research Institute, Fisheries Research Agency Japan. These samples have been collected by public fisheries institutes in the northeastern region of Japan since 1950 using a NORPAC net (0–150 m, 0.33 mm mesh). These samples were originally collected for routine monitoring of prey abundance for fisheries studies but they are in good condition and can be used for zooplankton species identification. The samples could be used for long-term quantitative analysis of the abundance and distribution of euphausiid eggs and larvae.

3.2.2 Distribution

There are two major current systems around Japan, the Oyashio Current and the Kuroshio Current. The area between these two currents in the NW Pacific Ocean is known as the mixed water region or the Kuroshio-Oyashio (K-O) transition (Fig. 3.2.1). There are 38 species of euphausiids reported to occur in Japanese waters, including both subtropical and subarctic species. There are 26 species of euphausiids that occur in the coastal area of northeastern Japan (Taki, 2007). *E. pacifica* is the most dominant species in this region, and *Thysanoessa inspinata* has the second highest abundance. Sampling along the A-line (five fixed stations in the Oyashio and mixed water region) in March, May, July and November, yielded 21 species of euphausiids (Okazaki, unpub. data) of which *E. pacifica* was the dominant taxon. Species diversity is higher toward southern stations. Results from cluster analysis suggested three species assemblages in this region: assemblages I, IIa, and IIb. Assemblage I occurred in the Oyashio region where the temperature at 100 m depth was 5°C or warmer.

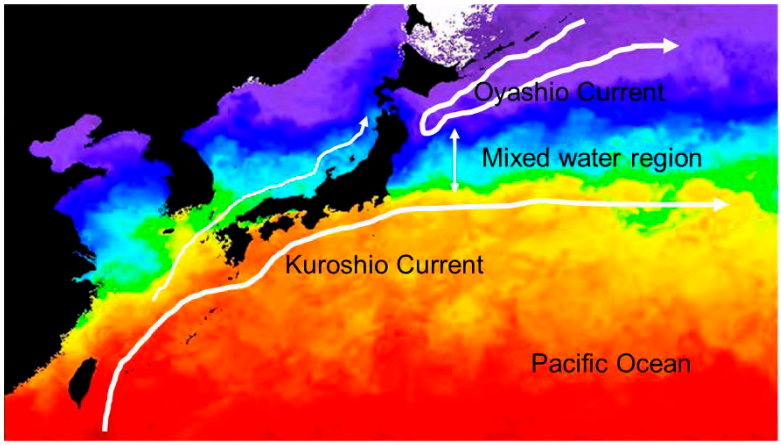

Fig. 3.2.1 Map of major currents around Japan: the Kuroshio Current (warm), the Oyashio Current (cold) and the mixed water region (K-O transition).

It consisted of five species – *E. pacifica, Thysanoessa inspinata, Thysanoessa longipes, Thysanoessa inermis*, and *Tessarabrachion oculatum*, *E. pacifica* was the dominant species (~88%), followed by *T. inspinata* (~10%). Assemblage IIa occurred year-round in the mixed water region where the temperature at 100 m depth was less than 5°C. There were nine species in this assemblage – *E. recurva, Nematoscelis microps, E. mutica, E. gibboides, E. tenera, E. hemigibba, Stylocheiron longicorne, E. similis*, and *Nematobrachion boopis*. Three species, *E. recurva, Nematoscelis microps,* and *E. mutica,* comprised over 75% of this assemblage. Assemblage IIb occurred in the mixed water region in summer and autumn. It consisted of six species – *Stylocheiron affine, S. carinatum, S. elongatum, Thysanopoda tricuspidata, Thysanopoda obtusifrons*, and *Euphausia brevis*. The three *Stylocheiron* species accounted for about 60% of this assemblage.

3.2.3 Seasonal Cycles

Egg and larval stages were found throughout the year but were especially abundant in spring (April to May). Adults occurred throughout the year and were particularly abundant in the Oyashio region from late summer through autumn (August to October). Abundance in the Oyashio was higher than in the mixed water region (Taki, 2004, 2006a,b). Individual *E. pacifica* and *T. inspinata* in the Oyashio region overwinter as juveniles, then mature, reproduce, and complete their life cycle in the following year (Kim *et al.*, 2009).

Abundance was determined using a variety of different techniques. On the krill fishing grounds, oblique tows using a 1.3 m diameter ring net obtained a maximum abundance of 100 ind. m^{-3} during the period from January to April. In other coastal areas of Japan, vertical tows using a 45 cm diameter NORPAC net found abundances of 0.2~0.5 ind. m^{-3}, with a maximum of 1 ind. m^{-3} year-round. In the subarctic domain (defined as areas where the temperature at 100 m depth is below 4℃), trawl tows in the summer found a mean abundance of 0.09 ind. m^{-3}, with a maximum of 0.62 ind. m^{-3}. Bongo net samples collected year-round on the A-Line in the Oyashio region found a mean of 0.29 ind. m^{-3} with a maximum of 2.4 ind. m^{-3}. Although krill abundances are known to be highly variable, it is likely that some of these differences may be attributed to differences in types of sampling gear.

3.2.4 Spawning

Egg and larval stages occurred throughout the year, but were especially abundant in spring (April to May). Reproductive activity occurs in close association with the timing of the spring bloom in both the Oyashio region and the K-O transition regions (Kim *et al*., 2010a).

Egg production experiments in the Oyashio region were conducted from March to July in 2007. No gravid females were found in March; however, they were present from April to July suggesting that *E. pacifica* spawning occurs from April to July with the peak period in April to May. *E. pacifica* spawning took place at low temperatures (<5°C). A total of n = 59 females spawned during these experiments (Fig. 3.2.2). The size range (total length, TL) of females in these experiments was 13–22 mm with most females in the 17–21 mm range, probably reflecting the size range of most mature females in the field. Individual brood sizes ranged from 4–183 eggs $female^{-1}$ with most brood sizes 5–120 eggs $female^{-1}$. There was no relationship between TL and brood size. A previous study on long-term fecundity of *E. pacifica* females found that smaller females produced smaller broods and larger females produced a wide range of brood sizes (Feinberg *et al*., 2007). The variability in the results from Japan suggests that individual variability among *E. pacifica* females in the Oyashio region is similar to that of *E. pacifica* in other geographical areas (Feinberg *et al*., 2007, 2013).

Combining the brood size data by experiment date suggests a decreasing trend in brood sizes from late April to June (Fig. 3.2.3). The experiment on April 25 contained 19 krill that spawned, with brood sizes of 8–183 eggs $female^{-1}$ and included n = 6 broods of more than 120 eggs. Because of varying numbers of spawning females in other experiments, the data are insufficient to validate this trend. It will be an interesting topic to investigate in future studies.

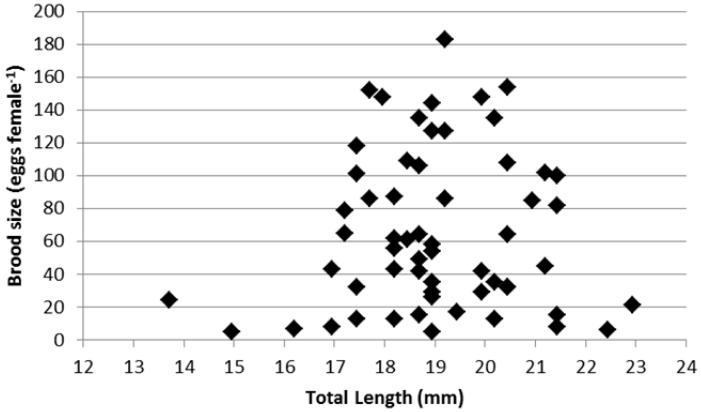

Fig. 3.2.2 Brood sizes (eggs per female) by total length of female from egg production experiments in the Oyashio region (March–July 2007).

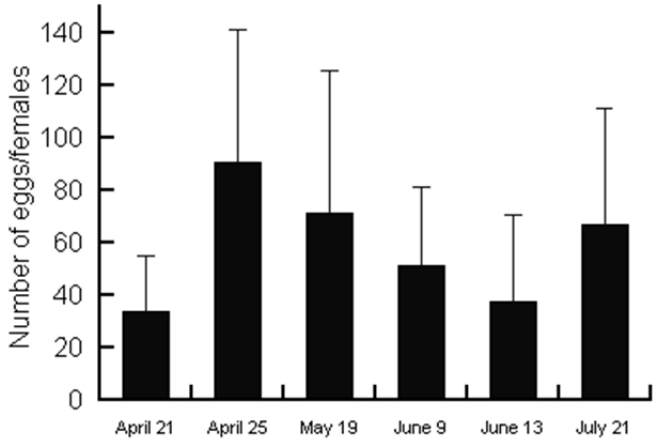

Fig. 3.2.3 Average number of eggs per female per experiment from egg production experiments in the Oyashio region (March–July 2007).

3.2.5 Species Composition and Growth in the Oyashio

The abundance and population structure of *E. pacifica* and *T. inspinata* were investigated during the period March 9 to April 29, 2007 at a single station in the Oyashio region as part of the Ph.D. research of Hye Soon Kim. Water temperatures and chlorophyll *a* concentrations varied from 1.1 to 6.1°C and from 0.02 to 6.3 mg m^{-3}, respectively, primarily reflecting the effects of varying mixtures of the water masses prevailing in this region. The abundance of euphausiids collected by oblique hauls with Bongo nets (0–200 m) at night ranged from 41 to 1040 individuals m^{-2} for *E. pacifica* and from 50 to 186 individuals m^{-2} for *T. inspinata*. Variations in the abundance of *E. pacifica* were related to water temperature and chlorophyll *a*, while abundance of *T. inspinata* varied only with temperature. Adults were the major component of both euphausiid stocks (>90% of the total). Modal size analysis revealed that a group comprising larger euphausiids of both species (*E. pacifica* 14–18 mm TL, *T. inspinata* 16–18 mm TL) occurred throughout the study period, often accompanied by one discrete group of smaller individuals (<11 mm TL for both euphausiid species), suggesting that the same euphausiid population is distributed throughout the heterogeneous water masses. Adult males were significantly smaller than adult females for *T. inspinata*, but this was not the case for *E. pacifica*. By tracking the progressive increase in the mean sizes of the larger size groups, growth rates were estimated to be 0.082 mm day^{-1} for *E. pacifica* and 0.022 mm day^{-1}

for *T. inspinata*. Full details are available in Kim *et al.* (2010a,b).

Growth of *E. pacifica* off northeastern Japan was estimated from size frequency distributions (Taki, 2004). This analysis showed that new cohorts appeared in April and grew slowly and steadily until the following March, then grew rapidly from March to June. This period of rapid growth in the spring is probably associated with the timing of the spring bloom. Results of the size frequency analysis indicate that the life span of *E. pacifica* in this region is 24 months for males and 28 months for females (Taki, 2004).

3.2.6 Lipid Analysis

As reported for *E. pacifica* by Saito *et al.* (2002), phospholipids (PL, 44.1–81.2%) such as phosphatidylethanolamine (PE, mean ± standard error, 26.1 ± 2.1%) and phosphatidylcholine (PC, 29.0 ± 2.3%) were found to be the dominant lipids. Compared to many other marine organisms, the level of PL was markedly high. The major fatty acids in the triacylglycerol (TAG) of *E. pacifica* were saturated fatty acids (SFA, 14:0 and 16:0), monounsaturated fatty acids (MUFA, 16:1 and 18:1), and polyunsaturated fatty acids (PUFA, 18:4 *n*−3 and 20:5 *n*−3, icosapentaenoic acid: EPA). The only fatty acids found in the tissue PL were SFA (16:0), MUFA (18:1), and PUFA (20:4 *n*−6, arachidonic acid: AA, EPA, and 22:6 *n*−3, docosahexaenoic acids: DHA). The comparatively high levels of 14:0, 16:0, 16:1 *n*−7, 16:2 *n*−4, 16:4 *n*−1, 18:1 *n*−7, 18:1 *n*−9, 18:4 *n*−3, and EPA in the TAG may be affected by the lipid composition of phytoplankton prey, such as diatoms which generally contain high amounts of these fatty acids. The levels of short chain 14:0, 16:1 *n*−7, 16:2 *n*−4, 16:4 *n*−1, 18:1 *n*−9, and 18:4 *n*−3 decreased in PL, while AA, EPA, and DHA increased. In particular, the levels of *n*−3 PUFA in PL were markedly high in all specimens. The mean proportion of EPA plus DHA accounted for more than 45% (55.0% in PE and 47.7% in PC) of the total fatty acids. These results suggest that *E. pacifica*, which contains markedly high levels of EPA and DHA, may biosynthesize these PUFA by carbon chain elongation and desaturation or selectively accumulate *n*−3 PUFA. In addition, their lipids may be an important source of *n*−3 PUFA for higher marine animals such as pelagic marine fishes (sardines, anchovies, and other small fishes) which mainly prey on these euphausiids. Marine fish accumulate high levels of *n*−3 PUFA because they are unable to synthesize DHA.

Lipids in krill sampled in Funka Bay (Hokkaido) in spring, summer, and winter in three consecutive years, 2000–2002 were analyzed by Kusumoto *et al.* (2004). They found that lipid content of the *E. pacifica* samples ranged from 5.1 to 11.6% on the basis of dry weight. Major lipid classes in samples from 2002 were triacylglycerols (TAG) (3.4–27.3%), free fatty acids (FFA) (6.9–22.2%), sterols (5.4–12.9%), phosphatidylethanolamines (PE) (3.4–17.5%), and phosphatidylcholines (PC) (36.2–53.8%). All of the samples analyzed for fatty acids were high in 16:0 (19.0–24.5% of total fatty acids), 18:1 *n*–9 (7.5–10.0%), 18:1 *n*–7 (6.3–8.1%), 20:5 *n*–3 (IPA) (15.3–24.7%), and 22:6 *n*–3 (DHA) (8.4–20.7%). The lipids of *E. pacifica* were found to be generally rich in PC and in IPA and DHA. Lipid content and proportion of TAG were higher in the spring samples than in the summer samples. The summer samples had higher concentrations of DHA in total fatty acids.

3.2.7 Genetics Studies

Analysis of regional gene structure (18S rDNA and 16S rRNA) of *E. pacifica* across the west–east subarctic Pacific showed only very small differences (Takahashi *et al.*, 2006). This finding suggests that *E. pacifica* throughout the subarctic Pacific could be considered the same population. If the lack of regional difference of gene structure in *E. pacifica* across the west–east Pacific is true and the euphausiids throughout this large geographic area constitute a single population, the life cycle and population dynamics of *E. pacifica* need to be considered on a large scale (*i.e.*, subarctic North Pacific).

3.3 People's Republic of China

An active and ongoing research program on the ecology of krill in the Yellow Sea is being undertaken primarily by scientists from the Institute of Oceanology Chinese Academy of Sciences – Key Laboratory of Marine Ecology and Environmental Sciences, based in Qingdao, China, and led by Prof. Song Sun. Regular sampling of krill on a quarterly-bimonthly basis was initiated in 2006 and these efforts continue. Sampling for krill is carried out with 80 cm ring nets with 500 µm mesh hauled vertically from near the sea floor to the surface (for juveniles and adults), with Henson egg nets and with large-volume whole water samplers for eggs and larvae of euphausiids, copepods, and other planktonic organisms. On some cruises, experiments are conducted on live krill for estimates of egg production, grazing, and metabolic rates.

3.3.1 Distribution and Seasonal Variability

Euphausia pacifica is the dominant species of euphausiid in the Yellow Sea. Three other species, *Pseudeuphausia sinica*, *P. latifrons* and *E. nana*, are abundant at times. The spatial distribution and population structure of *E. pacifica* in the Yellow Sea were studied from April 2006 through August 2007 (Sun *et al.* 2011, Liu *et al.* submitted) during eight cruises. *E. pacifica* is found throughout the Yellow Sea but its spatial distribution is controlled primarily by seawater temperature, with the adults preferentially inhabiting cold water. *E. pacifica* occurred throughout most of the study area in spring and winter. However, when sea surface temperatures were > 20°C in summer and autumn months, *E. pacifica* was mainly located in the Yellow Sea Bottom Cold Water (YSBCW) where the temperature below the thermocline was 8–10°C.

3.3.2 Diel Vertical Distribution

The vertical distribution and diel vertical migration of krill eggs and larvae were studied by Liu and Sun (2010) in a paper published in the special issue on krill biology and ecology in Deep-Sea Research Part II (Vol. 57, Issues 7–8). They studied stage-specific differences in the diel vertical distribution and migration of *E. pacifica* at a single station (E2, 70 m depth) in the southern Yellow Sea by sampling with a conical closing net from five discrete strata every three hours over a 24-h time period on May 2–3, 2001. Environmental data were collected simultaneously with net sampling. Results showed that eggs contributed a large proportion of the numerical abundance of the *E. pacifica* population throughout the investigation. They were mainly distributed below 20 m depth and concentrated in the 30–50 m strata throughout the day and night. Nauplius stage I (NI) was distributed below 10 m, and seldom occurred in the upper 10 m. Nauplius stage II (NII) and Metanauplius stage (MN) extended their distribution to nearly the whole water column; however, the MN resided somewhat shallower than NII. The majority of calyptopis stages I to III (CI to CIII) and early furcilia stages I to III (FI to FIII) were restricted to the upper 30 m throughout the day. The weighted mean depth tended to increase as the stage progressed from stage FI onward. Calyptopis stages showed weak or moderate diel vertical migration (DVM), and the onset of an obvious DVM took place at the FII stage. The amplitude of the DVM varied with developmental stages. Stages after FIV were often absent from samples during the investigation, but from the limited available data, DVM occurred in furcilia stages FIV–VI and female adults. Male adults showed a somewhat different migration behavior. In summary, an ontogenetic migration pattern is obvious from this high-frequency sampling: spawning took place at 20–50 m depth, hatched nauplii sank a little, metanauplii began moving toward the surface, and calyptopis larvae reached the uppermost layer. Furcilia larvae began DVM and deepened their daytime residence depth with age. The vertical distribution of *E. pacifica* seemed to relate to temperature and chlorophyll *a*.

3.3.3 Abundance

The seasonal cycle of abundance was investigated during cruises in 2006 and 2007. These efforts showed that juveniles and adults are widely distributed throughout the Yellow Sea in spring and winter when sea surface temperatures are 8–16°C.

Adults were found only in the YSBCW in summer and autumn. Average abundances of juveniles and adults by season are shown in Table 3.3.1. The one very high value of 243.8 individuals m^{-3} in autumn was at a single station. If this station were excluded, the range would be 0 to 18.7 individuals m^{-3}. These data are also shown in Fig. 3.3.1 as monthly values of abundance and biomass.

3.3.4 Spawning

From the same 2006 and 2007 cruises, eggs were sampled for the purpose of establishing the spawning season. Average egg abundances over the sampling region in March, April and May were 7.7, 57.6 and 32.5 eggs m^{-3}, respectively. The maximum abundance was in May 2007 (441.8 eggs m^{-3}). During June and August 2007, eggs were found at a few stations but with abundances of <3 eggs m^{-3}. Eggs were occasionally found in October and December suggesting that some egg production could occur nearly year-around, but that the main spawning season was clearly during the spring, in March–May. This is the same time of the year when chlorophyll concentrations are highest (Sun *et al*., 2011).

Table 3.3.1 Seasonally averaged abundances and range of values (number per cubic meter) for juveniles and adults in the Yellow Sea.

	Juveniles		Adults	
	Average (m^{-3})	**Range**	**Average (m^{-3})**	**Range**
Spring	0.28	0 – 6.3	0.46	0 – 2.8
Summer	0.32	0 – 2.1	0.65	0 – 9.5
Autumn	1.57	0 – 8.8	7.33	0 – 243.8
Winter	0.03	0 – 0.2	1.12	0 – 6.2

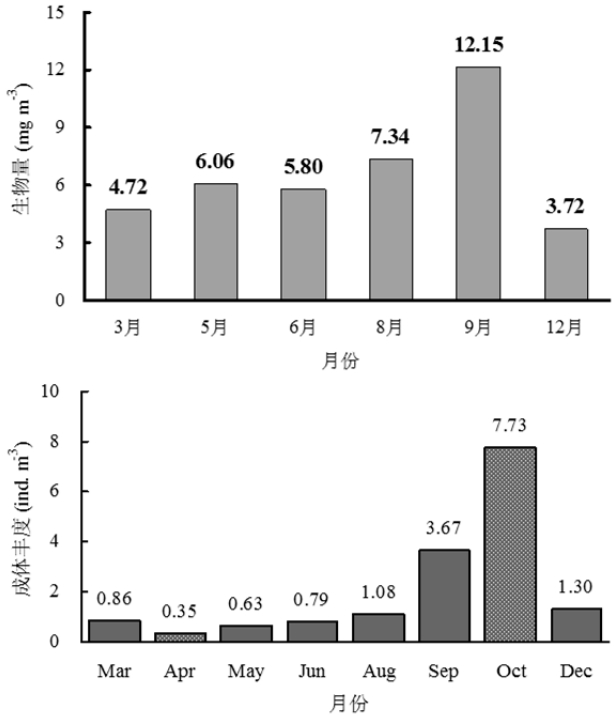

Fig. 3.3.1 Abundance (lower) and biomass (upper) of adult *Euphausia pacifica* in the Yellow Sea during the months indicated. See Sun *et al.* (2011) for details.

3.3.5 Recruitment

Larval stages were most abundant in spring, making up about 65% of the abundance of all stages (eggs, larvae, juveniles and adults) combined. Average abundance of larvae in spring was 40 m^{-3} whereas during summer, autumn and winter, numbers were on average from 0.3 to 1.0 m^{-3}. This suggests that, as with the abundance of eggs, spawning and recruitment are strongest in spring but minor amounts of spawning and recruitment may be occurring nearly year-round.

Results of these experiments showed that the brood sizes were highest in the spring, averaging 203.9 eggs $female^{-1}$ d^{-1} in April (2007) and 221.2 eggs $female^{-1}$ d^{-1} in May (2007). Lower values were found in March and June (71.3 and 25.3 eggs $female^{-1}$ d^{-1}, respectively). Maximum brood sizes were observed in May 2007, ranging from 69 to 485 eggs $female^{-1}$ d^{-1}. No spawning was noted during cruises in August, September, or December. This suggests that the main spawning season extends throughout the spring and apparently ends in late June. As noted above in the section on spawning

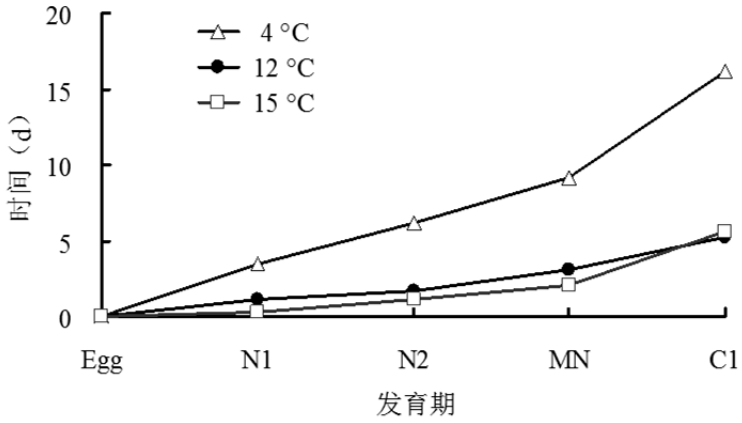

Fig. 3.3.2 Development times of larvae of *E. pacifica* at three temperatures. Note that these are the non-feeding stages of larvae. (*x*-axis = developmental sage, *y*-axis = number of days).

3.3.6 Life History Parameters

Developmental rates

Data on developmental rates for *E. pacifica* from the Yellow Sea are limited to a few measurements made on the non-feeding larval states (nauplius 1 and 2, metanauplius and calyptopis 1) at three temperatures (Fig. 3.3.2). Development was clearly related to temperature, with time from hatching to C1 at 4°C of about 16 days, compared to about 5 days at 12°C and 15°C. This compares well to Feinberg *et al.* (2006) who reported a median development time to C1 of 6.4 days at 10.5°C.

Egg production and brood sizes

To estimate egg production, on-board incubations of adult female *Euphausia pacifica* were conducted during eight cruises in 2006 and 2007 (Sun *et al*., 2011). A total of 181 females were incubated.

deduced from sampling of eggs in the sea, the spawning season can occur nearly year-round (based on the presence of eggs in the water column) but since no mature females were found in the field sampling, it appears that spawning is sporadic outside of the main spawning season.

Feeding and metabolism

Some euphausiid feeding studies have been conducted by Zhencheng Tao (Key Laboratory of Marine Ecology and Environmental Science, Institute of Oceanology – Chinese Academy of Sciences, Qingdao), using the disappearance of chlorophyll method, for both total chlorophyll and size fractions. Dr. Tao has also measured respiration rates and ammonia excretion rates of krill in incubations. The data from these studies are still being analyzed at the time of this report and will be published at a later date.

3.4 Republic of Korea

Ongoing euphausiid research is carried out as part of a project at the Korea Institute of Ocean Science and Technology (KIOST, formerly KORDI). The project is entitled 'The study on the impact of the Yellow Sea Cold Water Mass to the ecosystem (2009–2016)' **(**KIOST grant PE99165). The Yellow Sea bottom cold water mass (YSBCM: ≤ 10°C) persists in the deep central region of the Yellow Sea during the summer when the surface temperature increases to > 25°C. It may provide an over-summering refuge for cold water organisms (such as *Calanus sinicus*, and *Euphausia pacifica*) which enables them to maintain their populations in the Yellow Sea. Studies of the distribution, physiology, and feeding ecology of *E. pacifica* are included as part of this program. There are two annual cruises for this project: spring (April) and summer (August). Euphausiids are collected using either a conical net (mouth diameter: 1.5 m; mesh size: 333 or 417 μm) or mid-water trawl (square mouth: 2 m^2; mesh size: 417 μm). Sampling is conducted both day and night. Acoustics data are collected using a 200 kHz split-beam transducer (BioSonics, USA). Samples are collected to determine euphausiid abundance and biomass as well as for analysis of lipid composition. When possible, live euphausiid experiments are conducted during these cruises to measure molting rate and egg production (brood size) of *E. pacifica* using the protocol developed by the Peterson lab (available on the PICES website at http://www.pices.int/projects/Euphasiid/euphasiid.aspx).

3.4.1 Distribution

Adult krill are found predominantly in the middle of the Yellow Sea, which is the deepest part. However, they may occur just about everywhere in the Yellow Sea with the exception of the areas nearest to the coast. The vast majority of spawning occurs in the spring (April) but some eggs are found in the summer, especially in the coastal region of the southern part of the Yellow Sea. In general, eggs and adults are the dominant life stages in spring and juveniles and small adults are dominant in summer and fall. Results from the spring and summer of 2010 and 2011 show how this pattern may vary between years (Fig. 3.4.1). In the spring of 2010, eggs and early stage larvae (nauplii) were dominant at all stations, with adults present in low numbers. In the spring of 2011, furcilia, juveniles, and adults (including gravid females ≥ 2 cm total length (TL)) were abundant and engaged in active diel vertical migration (DVM) behavior. In the summer of 2010, the abundance of later-stage larvae (calyptopis and furcilia) increased, with some eggs and adults still present in the coastal region. Although they remained in the YSBCM, the krill maintained active DVM (from the bottom to below the thermocline), avoiding the high temperature water mass. In contrast, in the summer of 2011 the only euphausiids sampled were a few juveniles in the most southern part of the survey area (Fig. 3.4.1, bottom right panel). They did not show the same DVM pattern as observed in 2010. This may be a consequence of the episodic disturbance caused when Typhoon Muifa passed through the survey area just a couple of days before the research cruise.

3.4.2 Diel Vertical Migration

The Yellow Sea is a semi-enclosed marginal sea (mean depth = 50 m) and the waters are very warm in summer and fall. Adult krill are believed to take refuge from the warm temperatures in the colder bottom waters in the deepest parts of the Yellow Sea. Vertical movements of sound backscattering layers were followed for 24 hours with continuous acoustic surveys (targeting zooplankton) in spring and summer. Composition of the layers was confirmed with depth-targeted net sampling data. In spring, active DVM of *E. pacifica* was observed throughout the entire water column (Fig. 3.4.2, upper panel). In summer, DVM still occurred but was limited to the YSBCM, with the zooplankton avoiding the high temperature water mass (Fig. 3.4.2, lower panel). In the spring, the whole water column was well mixed and the Chl-*a* max was located in the surface layer. One backscattering layer was observed in the spring acoustic survey and it followed a typical diel vertical migration pattern. In summer, the water column was well stratified (well developed YSBCM) and the Chl-*a* max was located just below the thermocline. Acoustic surveys showed two backscattering layers during this survey. The first was found in the surface

mixed layer and appeared only at night. It comprised mainly fish larvae and small copepods. The second was located within the YSBCM and comprised mainly copepods and *E. pacifica*. This layer still showed a diel vertical migration pattern but it took place entirely within the YSBCM.

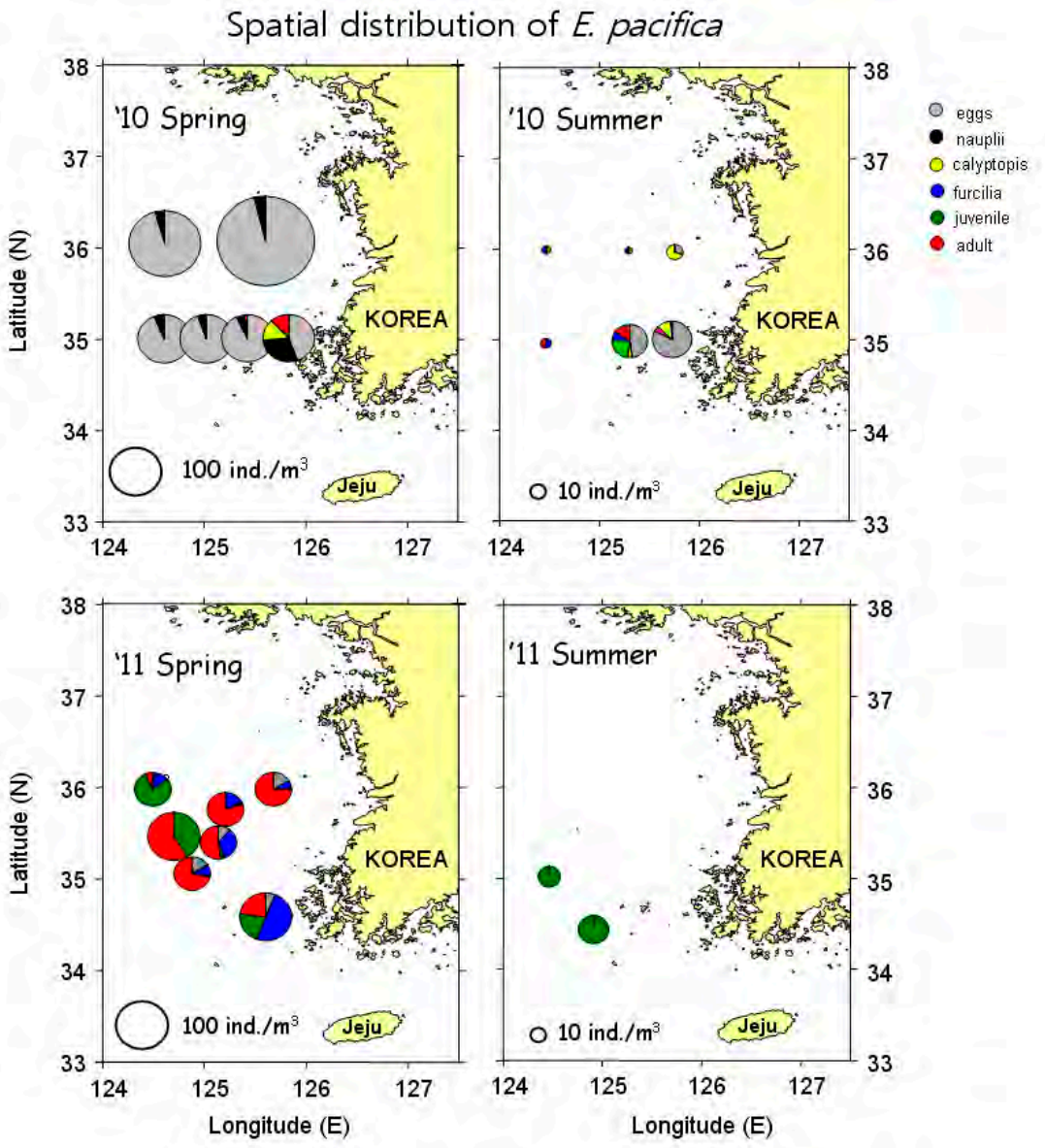

Fig. 3.4.1 Spatial distribution of the abundance of *Euphausia pacifica* with the relative composition of major life stages during spring and summer of 2010 and 2011. Conical nets were used for sampling in both years but the sizes were slightly different: 2010 – mouth diameter 1 m, mesh 330 μm, 2011 – mouth diameter 1.5 m, mesh 417 μm.

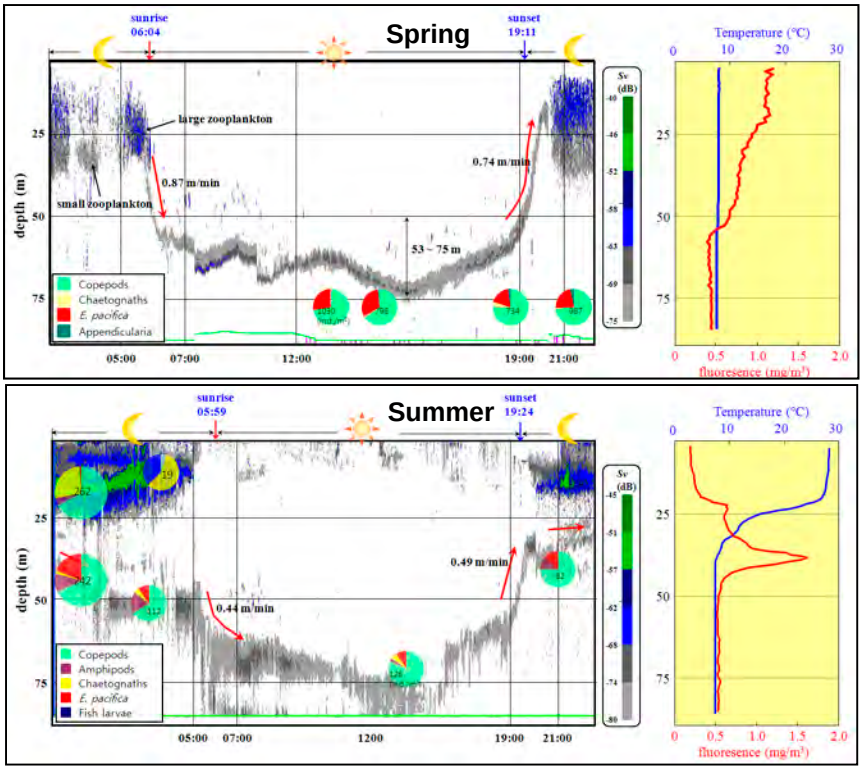

Fig. 3.4.2 Vertical movements of sound backscattering layers observed through a 24-h continuous acoustic survey (targeting zooplankton) in spring (upper panel) and summer (lower panel). Composition of the layers was confirmed with depth-targeted net sampling data. Temperature and fluorescence profiles show that the water column was well mixed in the spring and highly stratified in the summer.

3.4.3 Lipid Analysis

Lipids (including lipid class) and dietary lipid biomarkers (fatty acids and sterols) of *E. pacifica* collected from the Yellow Sea were analyzed to understand their energetics and dietary strategy. Lipid content was about 10% of dry weight and was similar between seasons (Fig. 3.4.3). Lipids serve as fuel for embryonic development and growth and also offset the potential for larvae to starve after hatching (Lee *et al*., 2006). Information on lipid storage and distribution in krill could provide insight into nutritional conditions as well as serve as an index of reproductive potential. *E. pacifica* from the Oregon and Washington coasts (OR/WA) allocate a significant amount of lipids to their eggs (4.5 µg egg^{-1}; Ju *et al*., 2006) and these are utilized for embryogenesis. No striking difference in lipid content and class composition (dominated by phospholipids and triacylglycerols) of adult *E. pacifica* between OR/WA and the Yellow Sea (YS) was found. Additionally, phospholipid (the major structural component of cell membranes) is the most abundant lipid class in krill from both regions, suggesting that phospholipids might be tightly linked with reproduction in *E. pacifica* as they are for other species (Hagen *et al*., 1996; Mayzaud *et al*., 2003; Ju *et al*., 2006, 2009). Based on the timing of reproduction and low storage lipid content, *E. pacifica* from OR/WA and YS probably employ similar reproductive strategies, at least in relation to brood size and energy budgets for reproduction. They only reproduce during periods (May to September in OR/WA and April in YS) when sufficient food is available because energy for reproduction (*i.e*., storage lipids) needs to be instantaneously obtained from what they ingest (*i.e*., phytoplankton blooms). However, lipid contents of adult krill in the YS in spring 2012 were slightly higher than those from other years and those from OR/WA (Fig. 3.4.3). This higher lipid content might be related to environmental conditions (*i.e*., abnormally low water temperatures during the previous winter, high food availability) and/or physiological status (pre-spawning) of krill at the time of sampling. Further investigation is required to understand the lipid dynamics of krill in relation to their life history strategies in the Yellow Sea.

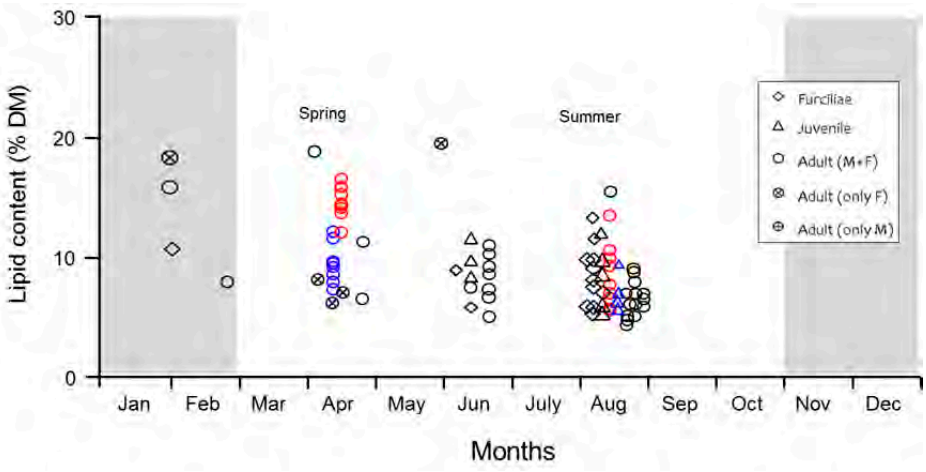

Fig. 3.4.3 Seasonal variation in the lipid contents of furcilia, juvenile, and adult *E. pacifica*. Graph includes specimens from the Oregon coast (black symbols) in comparison with specimens collected in the Yellow Sea in 2011 (blue symbols) and 2012 (red symbols).

3.4.4 Dietary Lipid Biomarkers

Results from dietary lipid biomarkers in conjunction with gut content analysis suggest that *E. pacifica* change their diet between spring and summer. This may be due to a seasonal change in the prey field or, as discussed above, this may be a result of the krill retreating to the YSBCM in response to increasing surface temperatures and thus encountering a different prey field. Diatoms (large-sized and chained) dominated the prey field in spring while small-sized particles were dominant during the summer (Fig. 3.4.4a,b). Krill fed mainly on diatoms in the spring but in summer they fed on any particles sized from 10 to 200 µm (protozoans, detritus, dinoflagellates, diatoms, *etc*., Fig. 3.4.4b). The grouped fatty acid results indicate a decrease in PUFA (algal origin) and an increase in BrFA (bacterial origin) between spring and summer (Fig. 3.4.4a), suggesting a shift in diet consistent with a change in residence depth.

The results from DVM behavior and diet composition strongly suggest that *E. pacifica* are making use of the YSBCM as an over-summering refuge by adapting their behavior through changes in their diet, their residence depth, and the depth to which they vertically migrate. This adaptation does not appear to necessitate any metabolic changes, such as diapause or reduction in metabolism.

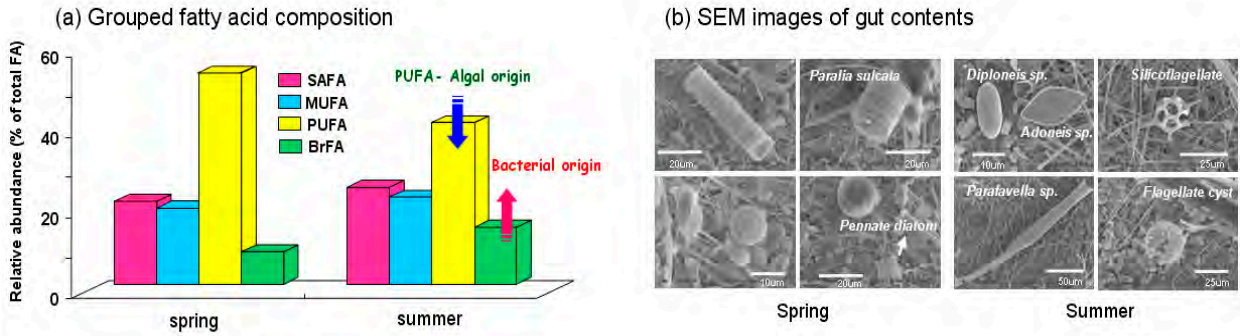

Fig. 3.4.4 (a) The relative abundance (%) of grouped fatty acids (SAFA: Saturated fatty acids, MUFA: Monounsaturated fatty acids, PUFA: Polyunsaturated fatty acids, BrFA: Branched and odd numbered fatty acids) in *E. pacifica* during spring and summer, 2010; (b) Selected SEM digital images of identified prey items in guts from *E. pacifica* adults sampled during spring and summer, 2010. Large-sized and chained diatoms were dominant in krill guts in spring; small diatoms, flagellates, protozoans, and detritus were dominant in summer.

3.5 Russia

Regular surveys have been conducted since 1985 in the western Bering Sea, the Sea of Okhotsk, the NW Pacific, and the Japan/East Sea, comprising a total area of ~6 million km^2 (Fig. 3.5.1). As of 2010 this included more than 100 expeditions with 25,000 trawls, 250,000 stomach samples, and 20,000 plankton samples. Standard methods of data collection and processing have been used for all expeditions. These regular broad-scale surveys provide information for large-scale monitoring of the status and dynamics of pelagic communities in these areas. Plankton samples are collected simultaneously with trawl catches of nekton. The majority of plankton samples have been collected with a Juday net (mouth 0.1 m^2, 168 µm mesh) from 200 m to the surface, or near the bottom to the surface in shallower areas. Some stratified sampling has been conducted to investigate vertical distribution. Samples are processed aboard the ship during the expedition using a size-fractioning method that has been standard at the Pacific Research Institute of Fisheries and Oceanography (TINRO-Centre) for the past 25 years. Data include total quantity of zooplankton, species composition, the role of each taxonomic group in the plankton community structure, biological information on the most abundant species, spatial distribution, vertical distribution, seasonal and inter-annual dynamics of the abundance of major taxonomic groups, estimates of stocks of zooplankton, estimates of the volume of zooplankton consumed by nekton, qualitative and quantitative characteristics of nekton, and diet composition of fish and squid. The current research effort does not include experiments on live zooplankton.

3.5.1 Distribution

Five species of euphausiid are found within the Russian study area: *Euphausia pacifica*, *Thysanoessa longipes*, *Thysanoessa inspinata*, *Thysanoessa raschii*, and *Thysanoessa inermis*. All five of these species were found in the Bering Sea and NW Pacific. *E. pacifica*, *T. longipes*, and *T. inspinata* were found further offshore in the NW Pacific, while *T. raschii* and *T. inermis* tended to be closer to the coast. Only two species, *E. pacifica* and *T. raschii*, were found in the Sea of Okhotsk. *T. raschii* was found throughout the Sea of Okhotsk while *E. pacifica* was found only in the southern portion. All five species were also found in the Japan/East Sea. *T. inermis* and *T. raschii* were closer to the coast while *E. pacifica*, *T. longipes*, and *T. inspinata* were found both near the coast and out into the center of the sea. The portion of the Japan/East Sea that shows no euphausiids was rarely sampled so the absence of euphausiids in these data may be due to the low number of samples collected in this region (Fig. 3.5.2).

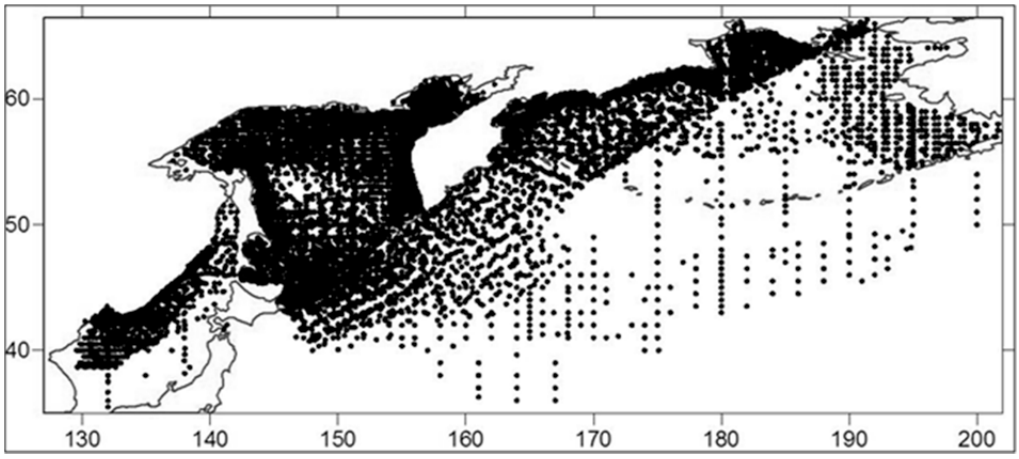

Fig. 3.5.1 Stations sampled for zooplankton by scientists from TINRO-Centre.

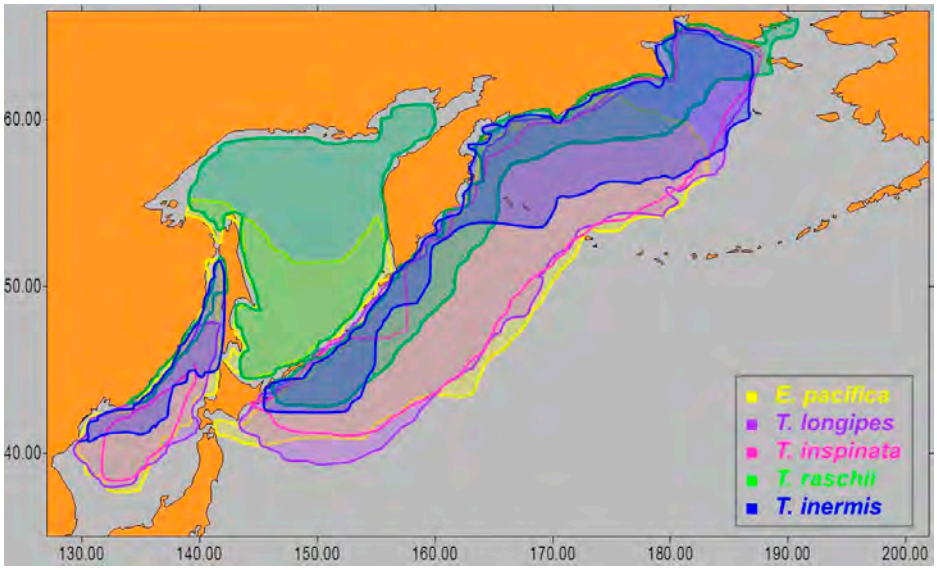

Fig. 3.5.2 Distribution of five species of krill in waters off Japan, Korea, and Russia for those regions sampled by Russia. The distribution of *Euphausia pacifica* is highlighted by the yellow line indicating that it is found in the Japan/East Sea and into the deeper waters of the Sea of Okhotsk as well as throughout the western Pacific and western Bering Sea. The Russian sampling area does not include the eastern Bering Sea but it is well known that *E. pacifica* is found there.

There is considerable overlap in the latitudinal range of euphausiid species in this area, but certain species seem to show a preference for certain habitats (Table 3.5.1). *E. pacifica* had the widest distribution over latitudinal and depth ranges. *T. longpies* and *T. inspinata* are both classified as boreal-arctic species, but *T. inspinata* was only found in waters up to 200 m deep while *T. longipes* was found in waters up to 2000 m deep. *T. inspinata* also remained in the more northerly region of the study area. *T. inermis* and *T. raschii* were found over a similar latitudinal range but segregated by water depth, with *T. inermis* occupying the shelf region and *T. raschii* occupying the neritic zone. *T. longipes*, *T. inspinata*, and *T. inermis* had similar spawning seasons (late winter to early summer) while *T. raschii* and *E. pacifica* started spawning in the spring and continued into the fall.

3.5.2 Seasonal Variability

Biomass

In the Bering Sea total euphausiid biomass on the inner shelf was <100 mg m^{-3} in winter and spring and ~200 mg m^{-3} in summer and autumn. On the outer shelf biomass was ~150 mg m^{-3} in winter, 300 mg m^{-3} in spring, 100 mg m^{-3} in summer, and just over 200 mg m^{-3} in autumn. In deep water the biomass was close to 100 mg m^{-3} in winter and spring and slightly lower in summer and autumn.

Table 3.5.1 Distributions, life spans, and spawning seasons of five species of euphausiids in the Russian study area.

Species	Length (mm)	Distribution	Latitude (°N)	Depth layer (m)	Life span (mo.)	Spawning season
T. longipes	25–36	Boreal-arctic species	34–52	0–2000	24–36	Feb–June
T. inspinata	15–23	Boreal-arctic species	42–52	0–200	24–30	Feb–June
T. inermis	20–45	Boreal-arctic shelf species	38–63	<300	24	Mar–June
T. raschii	20–30	Boreal-arctic neritic species	40–63	<100	24–36	April–Sept
E. pacifica	25–30	Wide boreal species	36–60	0–1000	12–21	May–Oct

In the Sea of Okhotsk total euphausiid biomass on the inner shelf was almost 400 mg m^{-3} in winter and spring, almost 600 mg m^{-3} in summer, and just over 200 mg m^{-3} in autumn. On the outer shelf, total biomass was 200 mg m^{-3} in autumn and winter, and ~400 mg m^{-3} in spring and summer. In deep water total biomass was ~200 mg m^{-3} in winter, spring, and summer, and almost 600 mg m^{-3} in autumn. The abundance of *T. raschii* and *T. longipes* in the Sea of Okhotsk was related to the thickness and extent of the ice cover, with *T. raschii* dominant on the shelf and *T. longipes* dominant in deep water.

In the NW Pacific, euphausiid biomass was essentially zero on the inner shelf during all seasons. In outer shelf waters the biomass was ~80 mg m^{-3} in winter, 50 mg m^{-3} in spring, and about 125 mg m^{-3} in summer and autumn. In deep water the biomass was 50 mg m^{-3} in winter, 25 mg m^{-3} in spring, ~60 mg m^{-3} in summer, and ~125 mg m^{-3} in autumn.

In the Japan/East Sea euphausiid biomass was low on the inner shelf (<25 mg m^{-3}) in all seasons. On the outer shelf the biomass was <50 mg m^{-3} in winter and ~70–90 mg m^{-3} in spring, summer, and autumn. In deep water the euphausiid biomass was ~100 mg m^{-3} in all seasons.

Early life stages

Abundance data (indiv. m^{-3}) for early life stages (eggs, calyptopis, furcilia <3 mm) of all species of euphausiids were combined by season and region to provide an idea of general trends in these areas (Table 3.5.2). Abundances were highest in all regions during the summer, and decreased into autumn and winter. Although this pattern was consistent among all regions, winter abundances were still relatively high in the NW Pacific region (9.78 indiv. m^{-3} *vs.* <1 indiv. m^{-3} in other regions). In all seasons, abundances tended to be higher in the Sea of Okhotsk and the NW Pacific and lower in the Bering Sea and Japan/East Sea. Juvenile euphausiids were found in the upper portion of the water column throughout the year in all four regions.

3.5.3 Diel Vertical Migration

Comparison of day and night samples of the upper 50 m and upper 200 m of the water column clearly indicates diel vertical migration in all four regions of the study area. Nighttime euphausiid abundance was ten times higher than daytime abundance in the upper 50 m and four times higher than daytime abundance in the upper 200 m of the water column. Migrations were weaker in the more northerly areas during the summer when the nighttime period was <3 h. Samples collected at night definitely provide a more accurate estimate of euphausiid abundance.

3.5.4 Caloric Content

Caloric content (calories (g wet wt.)$^{-1}$) was measured for four species of euphausiids in three regions of the Russian study area (Table 3.5.3). Results were obtained for some species for spring, summer, and autumn while others were measured in one or two of these seasons. These data are of interest to investigate the quality of euphausiids as a food source and whether that quality varies seasonally. Seasonal data for adult *T. longipes* and *T. raschii* from the Sea of Okhotsk show that *T. raschii* caloric content was similar in all three seasons, while that of *T. longipes* was decidedly higher in summer and autumn. Caloric content of *T. inermis* in this region also increased considerably between summer and autumn, suggesting that these two species may constitute an important quality food source for other animals, including commercially important species, at this time of year.

Table 3.5.2 Seasonal distribution of early life stages of euphausiids (eggs, calyptopis, furcilia <3 mm (indiv. m^{-3}, all species combined)). Juvenile euphausiids were found in the upper portion of the water column throughout the year in all four regions.

	Spring	Summer	Autumn	Winter
Bering Sea	6.95	9.12	3.87	0.15
Sea of Okhotsk	37.25	52.38	16.25	0.21
NW Pacific	25.05	39.25	15.33	9.78
Japan/East Sea	14.48	8.45	5.78	0.23

Table 3.5.3 Caloric content of euphausiids (calories (g wet wt.)$^{-1}$) from the Sea of Okhotsk, Japan/East Sea, and Bering Sea in spring, summer, and autumn.

Area	Species	Spring	Summer	Autumn
Sea of Okhotsk	*E. pacifica*	–	–	1183
	T. inermis	–	932	1269
	T. longipes (adult)	1136	1414	1375
	T. longipes (juvenile)	950	–	–
	T. raschii (adult)	1094	1085	1098
	T. raschii (juvenile)	730	–	–
	T. raschii (larvae)	627	–	–
Japan/East Sea	*E. pacifica*	–	–	986
	T. inermis	–	–	994
Bering Sea	*T. longipes*	–	1271	–

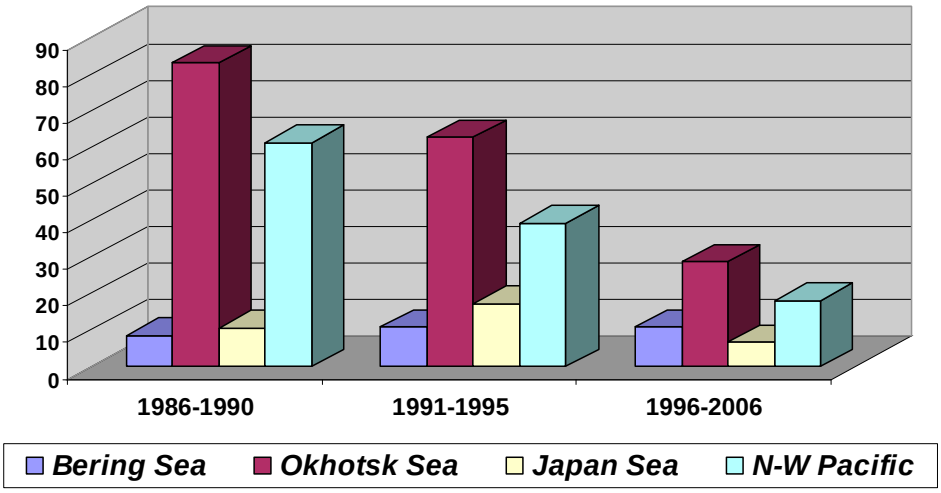

Fig. 3.5.3 Abundance of all euphausiids (in millions of tons) in four regions – western Bering Sea, Okhotsk Sea, Japan/East Sea and NW Pacific Ocean. Stocks in the Bering Sea and Japan Sea appear to be fairly stable while stocks in the Okhotsk Sea and the NW Pacific show a declining trend in abundance.

3.5.5 Long-term Variability of Euphausiid Stocks

The status of euphausiid stocks in four regions (the western Bering Sea, Sea of Okhotsk, Japan/East Sea and NW Pacific Ocean) have been evaluated as one component of the Russian zooplankton studies (Fig. 3.5.3). Results of the Russian sampling program show that total euphausiid stocks in the Sea of Okhotsk and the NW Pacific were extremely high in the period from 1986–1990 and have been gradually decreasing since then (Fig. 3.5.3). Stocks in the Bering Sea and the Japan/East Sea are lower overall but have not changed appreciably in the period from 1986–2006. This suggests that these stocks, while lower overall, are more stable than the stocks in the Sea of Okhotsk and the NW Pacific.

3.6 United States of America

Krill on the west coast of the United States are sampled routinely in southern California by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program, in central California by scientists from the University of California at Santa Cruz and others, in the northern California Current off Newport, Oregon, by scientists from NOAA and Oregon State University, and in waters off Baja California, Mexico, by scientists from CICESE (Centro de Investigación Científica y de Educación Superior de Ensenada).

3.6.1 Sampling Programs

Southern California: *CalCOFI Program*

A grid of approximately 60 hydrographic stations has been sampled quarterly since 1949 (Fig. 3.6.1) with some brief gaps in the 1970s. For details, see http://www.calcofi.org. Bongo net samples are collected routinely in oblique tows from the surface to 210 m depth. Euphausiids have been enumerated from the samples collected at night in winter and spring of each year. From these samples, interannual variations in abundance have been elegantly described by Brinton and Townsend (2003) in a paper which compares samples from central California, southern California, and Baja California. Germane to this report are the data on *Euphausia pacifica* which show quite clearly that this is a cold water, widespread, oceanic species whose larval and juvenile stages are common in coastal waters. *E. pacifica* is the most abundant krill species in these samples and biomass is significantly negatively correlated with the Pacific Decadal Oscillation (PDO) with biomass higher when the PDO is negative. Typical densities are on the order of 2000 individuals 10 m^{-2} (Brinton and Townsend, 2003), which is equivalent to 200 individuals m^{-2} or 1 m^{-3} when averaged over a 200 m water column. Recent work by Di Lorenzo and Ohman (2013) suggests that biomass and sea surface height have a higher correlation than biomass and the PDO. The major El Niño events in 1957–58, 1982–83, 1992–93, and 1997–98 were associated with negative biomass anomalies.

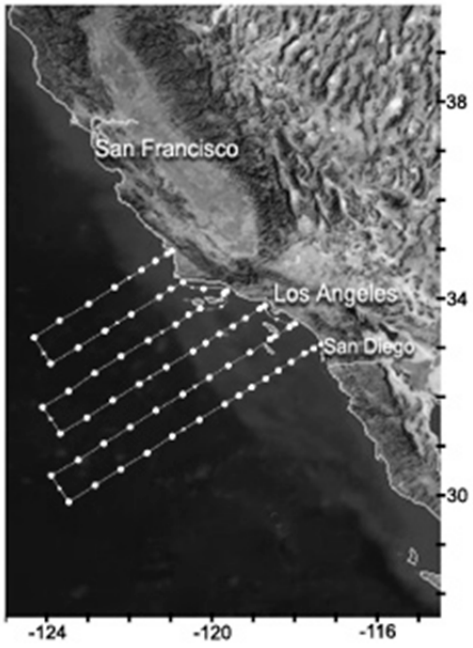

Fig. 3.6.1 The CalCOFI sampling grid off southern California.

Central California: ***University of California at Santa Cruz***

The distribution of two krill species, *E. pacifica* and *Thysanoessa spinifera*, were studied in Monterey Bay in relation to the distribution and foraging behavior of blue whales (Croll *et al*., 2005). Krill distributions were mapped using both Bongo nets and high frequency acoustics (Simrad EY-500 echosounder operating at 200 kHz). Results of this work suggested that the lengths of krill captured in Bongo nets were smaller than the lengths of krill estimated from whale feces (mean lengths of *E. pacifica* and *T. spinifera* eaten by whales were 16.0 and 19.3 mm, respectively, as compared to 11.8 and 16.3 mm in the Bongo net samples). The krill were extremely patchy and occurred mostly in schools associated with Monterey Canyon. Mean density of individual krill was 1.3 g wet weight m^{-3} or 39 individuals m^{-3}; schools associated with the Canyon itself reached densities of 153 g wet weight m^{-3} or 4403 individuals m^{-3}.

Central California: ***Gulf of the Farallones***

Krill have been sampled during May–June as part of a central California survey of juvenile rockfish over the past 20+ years. The distribution and abundance of krill captured in rockfish trawls (12 m × 12 m mouth; 9 mm cod end liner) have been studied along with backscatter signals from a Simrad EK500 echosounder operating at 38, 120 and 200 kHz (Santora *et al*., 2011a,b). These results clearly show that krill have affinities for particular bathymetric and hydrographic habitats (*i.e*., canyons, isobaths, fronts, Fig. 3.6.2), but it is unclear how these factors collectively influence krill aggregations. The rockfish surveys provided the opportunity to look at the detailed spatial distribution of krill (chiefly *E. pacifica* and *T. spinifera*) using hydroacoustics in central-northern California waters. Distributions were investigated in relation to bathymetric slope, distance from shelf break/canyon heads and fronts, phytoplankton/Chl-*a* persistence, and sea surface height anomalies (eddy structures). This type of work will be extended into waters off Oregon and Washington through the Ph.D. research of Elizabeth Phillips and her advisor, John Horne, University of Washington.

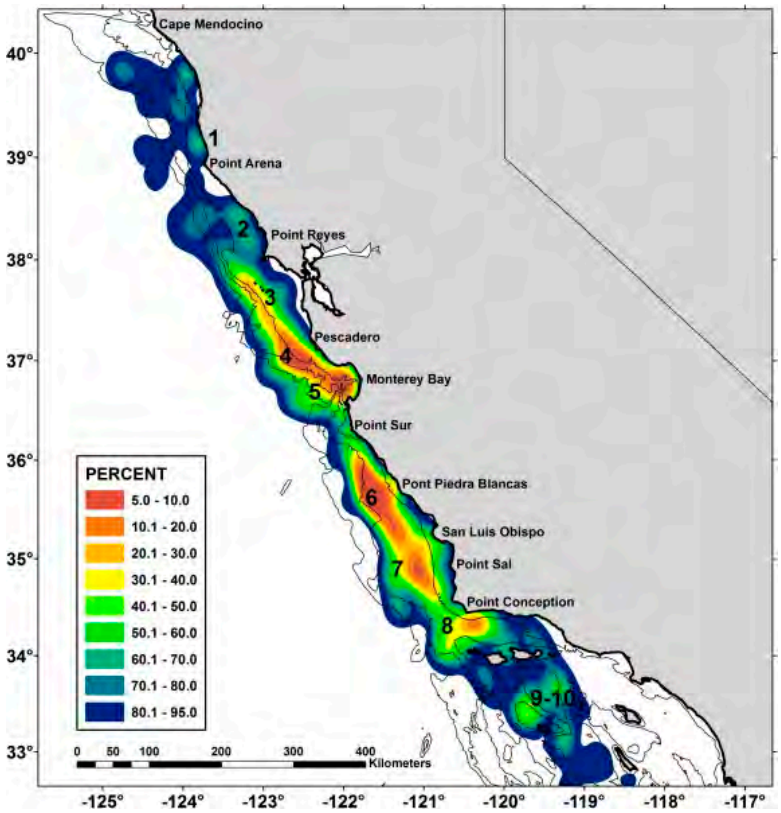

Fig. 3.6.2 Location of krill hot spots off central California.

Oregon: *The Newport Time Series*

The Newport time series was established in 1996 and is based on biweekly cruises off Newport, Oregon (44°40′N). Seven stations are sampled across the continental shelf and slope, at distances of 1, 3, 5, 10, 15, 20, and 25 nautical miles from shore with water depths ranging from 20 to 300 m. Sampling includes a CTD profile (Seabird 19 (pre-2010), Seabird 25 (2010–present) with WetStar fluorometer and Seabird 43 oxygen sensor), Secchi disc depth, surface water samples for chlorophyll, nutrients, and phytoplankton species composition, a vertical plankton net tow (½ m diameter 200 µm mesh net) from 100 m depth to the surface (5 m off the bottom to the surface in shallower waters) and an oblique Bongo tow (60 cm diameter, 333 µm mesh net) through the upper 25 m of the water column. Since 2001, cruises have been conducted at night whenever possible to facilitate the collection of adult euphausiids. During the nighttime cruises, euphausiids from one side of the Bongo tow are preserved and those from the other side are used for live animal experiments. Individual krill are incubated in 500 ml or 1 L jars for molting rates (30–60 individuals) and brood size measurements (up to 20 females). Animals are also transported to the shore laboratory on an *ad hoc* basis for other experiments which have included developmental rates, long-term variations in brood size and interbrood periods, grazing rates, and physiological analyses including carbon content and lipid composition. Data on distribution and abundance of copepods, euphausiid eggs, larvae, juveniles and adults from these cruises are supplemented by a wealth of historical data on hydrography, copepods, and euphausiids from samples collected in 1969–1973, 1983, 1990–1992 (copepods and euphausiid eggs and larvae), 1963–1967 (Smiles and Pearcy, 1971), and 1971–1972 (juvenile and adult euphausiids; Gómez-Gutiérrez *et al*., 2005).

Oregon: *The GLOBEC LTOP Time Series*

The Peterson lab also sampled copepods and euphausiids at ~40 stations, ranging from 1–85 nautical miles from shore and water depths to ~4000 m along five transects from Newport south, in February, April, July, September and November from 1998–2003 as part of the GLOBEC Long Term Observation Program (LTOP) cruises. Physical, chemical, and chlorophyll data from these cruises are available online at http://ltop.oce.orst.edu/~ctd/index.html. In addition, the Peterson lab sampled zooplankton at ~100 stations during each of four GLOBEC "mesoscale" cruises (MESO; June and August 2000 and 2002) and mapped oceanographic features and zooplankton from Newport to Crescent City to resolve finer-scale and feature-specific copepod and krill distribution and abundance associated with eddies, meanders, the upwelling jet, and upwelling filaments. For both the LTOP and MESO cruises, zooplankton samples were collected with a ½ m diameter (200 µm) net towed vertically from 100 m depth to the surface, and a 1 m^2 MOCNESS (333 µm) with ten nets in depth-stratified tows from 500 m depth to the surface.

Seward Line in Alaska: *U.S. GLOBEC LTOP Time Series*

U.S. GLOBEC's Northeast Pacific program also supported Long Term Observations along the Seward Line, a set of hydrographic stations first established in the 1960s by the University of Alaska (and Dr. Tom Royer). GLOBEC studies emphasized work on the biology and ecology of juvenile salmon, dominant euphausiid species, several species of large copepods, and forage fish (salmon prey) in coastal regions of the North Pacific. Studies focused on how these populations are controlled by climatically variable physical forcing, especially at large- to meso- scales. Goals were to quantify the importance of (a) local primary and secondary production, and (b) imported secondary production (*e.g.*, cross-shelf import of large-bodied zooplankton (copepods and euphausiids) from deeper offshore waters in spring) for providing rapid growth and/or high survival of juvenile pink salmon in coastal waters of the Gulf of Alaska. Target species of invertebrates were copepods (*Calanus pacificus* and *C. marshallae*) and the euphausiids *E. pacifica* and *T. spinifera*. Station locations sampled along the Seward Line are available in GLOBEC planning documents, and also in Coyle and Pinchuk (2005) and Pinchuk and Hopcroft (2006).

3.6.2 Spatial Distribution

Throughout the California Current, from Mexico to Canada, *Euphausia pacifica* is primarily a continental slope and oceanic species. During the upwelling season though, adults may be found in shelf waters. Eggs and larvae are generally far more abundant in shelf waters than slope waters off Oregon (Gómez-Gutiérrez *et al*., 2005) and this is likely true elsewhere in the California Current.

3.6.3 Vertical Distribution

Shelf waters

The vertical distribution of *E. pacifica* eggs, larvae, juveniles and adults was examined using MOCNESS samples collected off the Oregon coast in both shelf and slope waters at several stations near Newport during 1998–2003. Figure 3.6.3 illustrates the changes in vertical distribution between day and night at three shelf stations near the Rogue River (RR) and Heceta Head (HH). In two of the three MOCNESS tows, eggs were found within the upper 25 m while in the third, the weighted mean depth of eggs was 110 m. The presence of eggs at depth could mean that they were laid at depth or that they sank to that depth from surface waters. Either scenario could apply in this instance since eggs can sink at a rate of ~120 m per day and hatching times are ~40 h. Given these parameters, eggs could easily sink to a depth of 110 m before hatching.

The nauplius and calyptopis stages show evidence of sinking at night whereas the furcilia stages show evidence of diel vertical migration starting at the FIII or FIV stages (Fig. 3.6.3, life stages 6 and 7), with pronounced diel vertical migrations at the FVII stage (life stage 10) as well as for juveniles and adults.

Slope waters

Vertical distributions of eggs in four MOCNESS tows at slope stations were considerably different from shelf stations, with eggs found deeper than 125 m at all four stations (Fig. 3.6.4). Nauplii (life stage 2) were not found at these stations. Calyptopis and furcilia stages I–VI were restricted to the upper 50 m by day whereas the furcilia VII, juveniles and adults were below the mixed layer by day. By night, eggs were again at depths greater than 150 m. In this case, it seems more likely that the eggs were laid at depth, although at a sinking rate of 120 m per day it would be possible for them to sink from the surface to a depth of 200 m before hatching.

Diel vertical migration is evident beginning with Furcilia stage II (Fig. 3.6.4, life stage 5) although this behavior is most pronounced for FVII (life stage 10), juveniles, and adults.

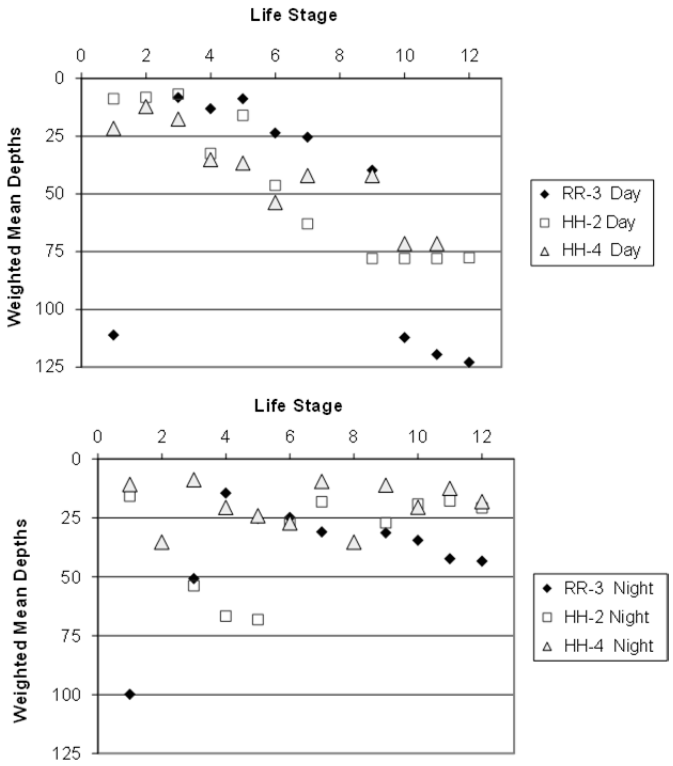

Fig. 3.6.3 Vertical distribution of life cycle stages of *Euphausia pacifica* in shelf waters off Oregon by day (top panel) and night (bottom panel). Life stages are indicated numerically with 1 = embryos, 2 = nauplii, 3 = calyptopis, 4–10 = furcilia I–VII, 11 = juveniles and 12 = adults. Stations are off the Rogue River (RR) and Heceta Head (HH).

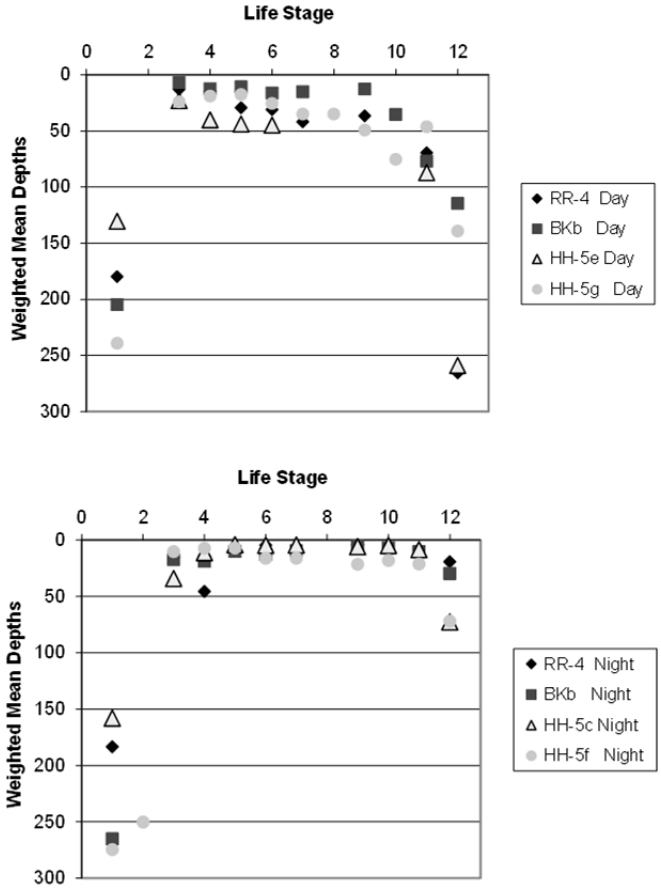

Fig. 3.6.4 Vertical distribution of life cycle stages of *E. pacifica* in slope waters off Oregon by day (top panel) and night (bottom panel). Life stages are indicated numerically with 1 = embryos, 2 = nauplii, 3 = calyptopis, 4–10 = furcilia I–VII, 11 = juveniles and 12 = adults. Stations are off the Rogue River (RR) and Heceta Head (HH).

3.6.4 Seasonal Cycle of Spawning

Off Oregon, the first spawning event for *E. pacifica* generally occurs in the spring, with densities of eggs up to several hundred per cubic meter. However, spawning behavior is most intense in July and August, which are the peak months of upwelling. Peaks in egg densities range from 1000 to 2000 m^{-3} (Feinberg and Peterson, 2003). *T. spinifera* spawn prior to and during upwelling, but with no intense period as seen for *E. pacifica*. Peaks in *T. spinifera* egg densities are always lower than for *E. pacifica*. Further details are presented below in the section on brood sizes.

3.6.5 Seasonal Cycles of Abundance

Seasonal cycles of abundance are probably best understood for the Oregon study area due to the biweekly year-round sampling program. Sampling on a broader temporal scale (such as quarterly sampling by the CalCOFI program) does not allow for robust resolution of seasonal cycles. The seasonal cycle of abundance off Newport is shown in Figure 3.6.5. Noteworthy features are that adults and juveniles are seldom found in continental shelf waters (Stations NH05 and NH15) but when they do occur, it is only during the summer upwelling season.

In offshore waters (Station NH25), adults are at least one order of magnitude more abundant than at the shelf stations. Abundances of eggs are similar among stations and are highest during the summer upwelling season. Early life history stages (nauplii, calyptopis and furcilia) are present throughout much of the year.

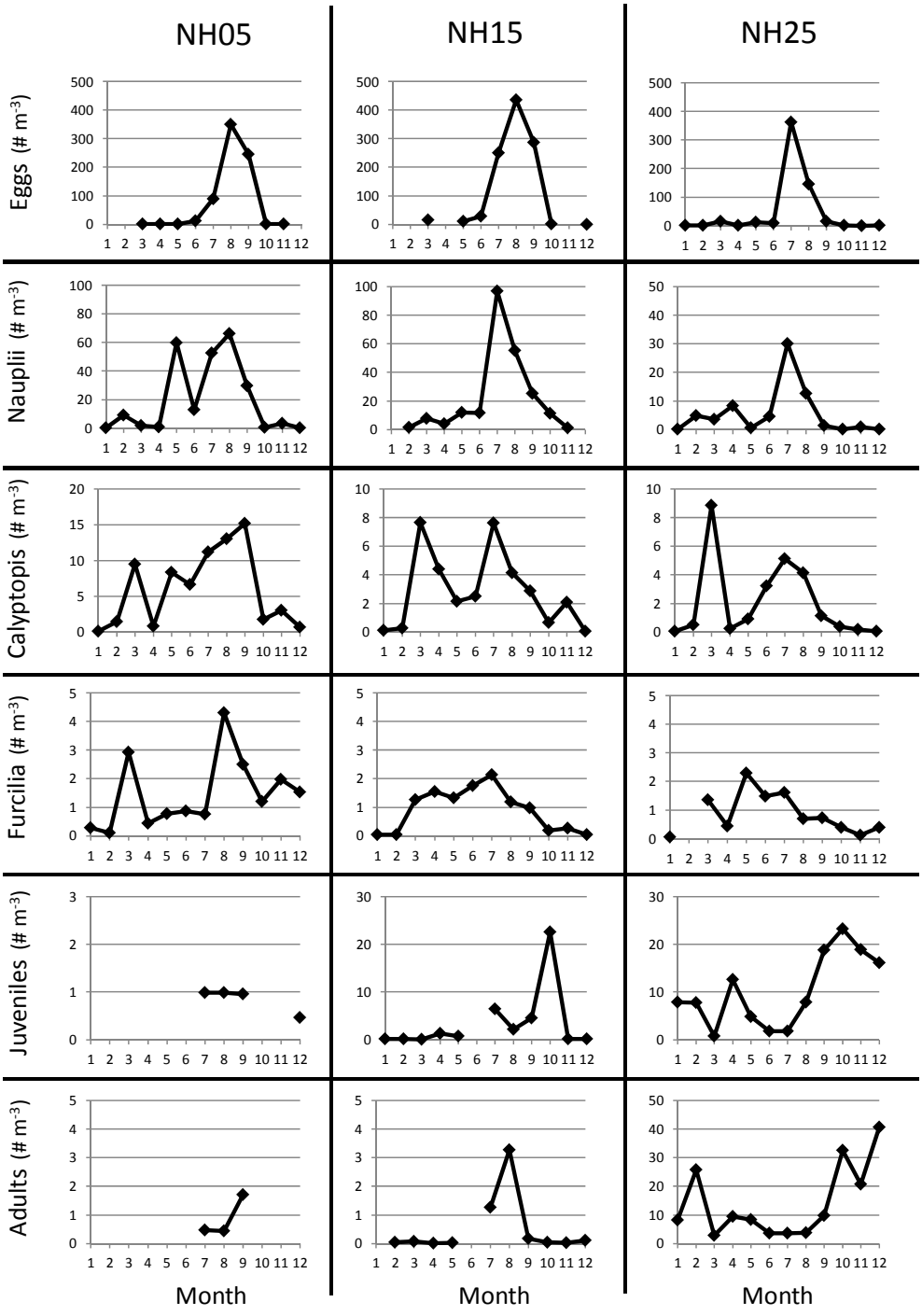

Fig. 3.6.5 Climatological abundances of *E. pacifica* eggs, nauplii, calyptopis, furcilia, juveniles, and adults at three stations off Newport averaged for the period from 2001–2006. Water depths at these stations: NH05 is 62 m, NH15 is 92 m and NH25 is 296 m.

3.6.6 Life History Parameters

Development time and developmental rates

In order to estimate vital rates such as growth, productivity, and mortality from field data, it is essential to have accurate information about development time to a given life stage and the duration of time spent at that stage. To measure development time of *E. pacifica* off Oregon, gravid adult females were collected and transferred to the laboratory where females spawned, eggs hatched, and larvae were reared at 10.5°C. Four cohorts of larvae were fed to excess with a combination of phytoplankton species and monitored daily until they reached the juvenile stage. The euphausiids were maintained separately (one individual per jar) from the third furcilia (FIII) to the juvenile stage to observe developmental pathways.

Individual cohorts developed at nearly the same rate until the first furcilia (FI) stage, after which two cohorts began to develop significantly faster than the others. Median time to the juvenile stage ranged from 51.9 to 60.6 days, with significant differences among cohorts. The first calyptopis stage and the third furcilia stage lasted longer than any other stages and appear to be bottlenecks in the development of this species. Individual development from FIII to juvenile varied widely both within and among cohorts but most individuals followed one of four main developmental pathways. Over half of the euphausiids skipped one development stage between FIII and juvenile (58%), although none skipped more than one stage. There was no tendency for individuals from the same cohort to follow the same developmental pathway. This variability in development may be even higher in the field and could impact mortality calculations and cohort analysis from field samples. For full details of this study see Feinberg *et al.* (2006). Figure 3.6.6 shows the median time to each development stage at three temperatures. Data for 8° and 12°C represent medians from all experiments at those temperatures (Ross, 1981) and data at 10.5°C represent the median for Cohorts 1, 2, and 3 from Feinberg *et al.* (2006). These results from two different studies suggest that the developmental rate is strongly dependent on temperature.

Brood sizes

Brood sizes of female *E. pacifica* based on measurements made off Newport, Oregon, were published by Gómez-Gutiérrez *et al.* (2006). This work has been updated as a Working Group 23 synthesis product (Feinberg *et al.*, 2013, Journal of Plankton Research, in press) in which *E. pacifica* brood sizes were compared at eight locations around the Pacific Rim: southern California and northern California Current, Newport Line, Puget Sound, Gulf of Alaska, the Oyashio, Toyama Bay, and the Yellow Sea (Fig. 3.6.7). Brood sizes for *E. pacifica* were highly variable in all regions and ranged from 5 to 697 eggs female^{-1} overall. Median brood sizes were largest in the Yellow Sea and off Newport; maximum brood sizes were largest by far in the regions off the coasts of Oregon and Washington,

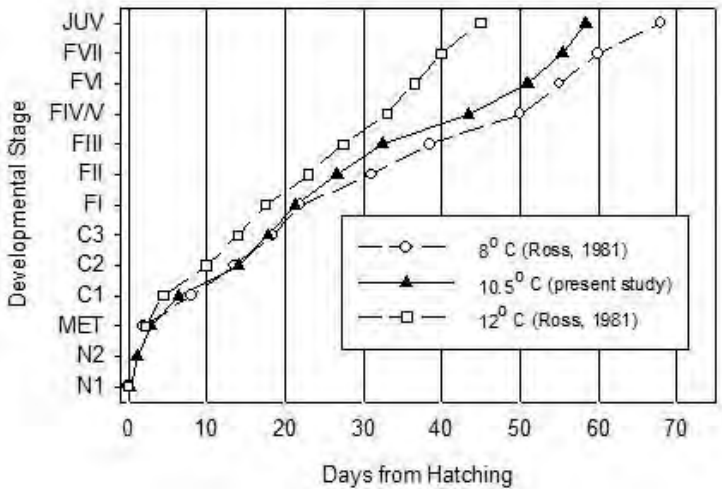

Fig. 3.6.6 Developmental times for *E. pacifica* in the laboratory from Ross (1981) and Feinberg *et al.* (2006).

and the Yellow Sea. Quantile regression analysis revealed that there was a significant relationship between female length and brood size at the 95% quantile for broods from southern California, Oregon, and Washington, as well as Toyama Bay, Japan. This suggests that factors such as hydrographic conditions, food quantity/quality, and physiological condition of females might limit brood sizes more in the regions where female length is not a limiting factor.

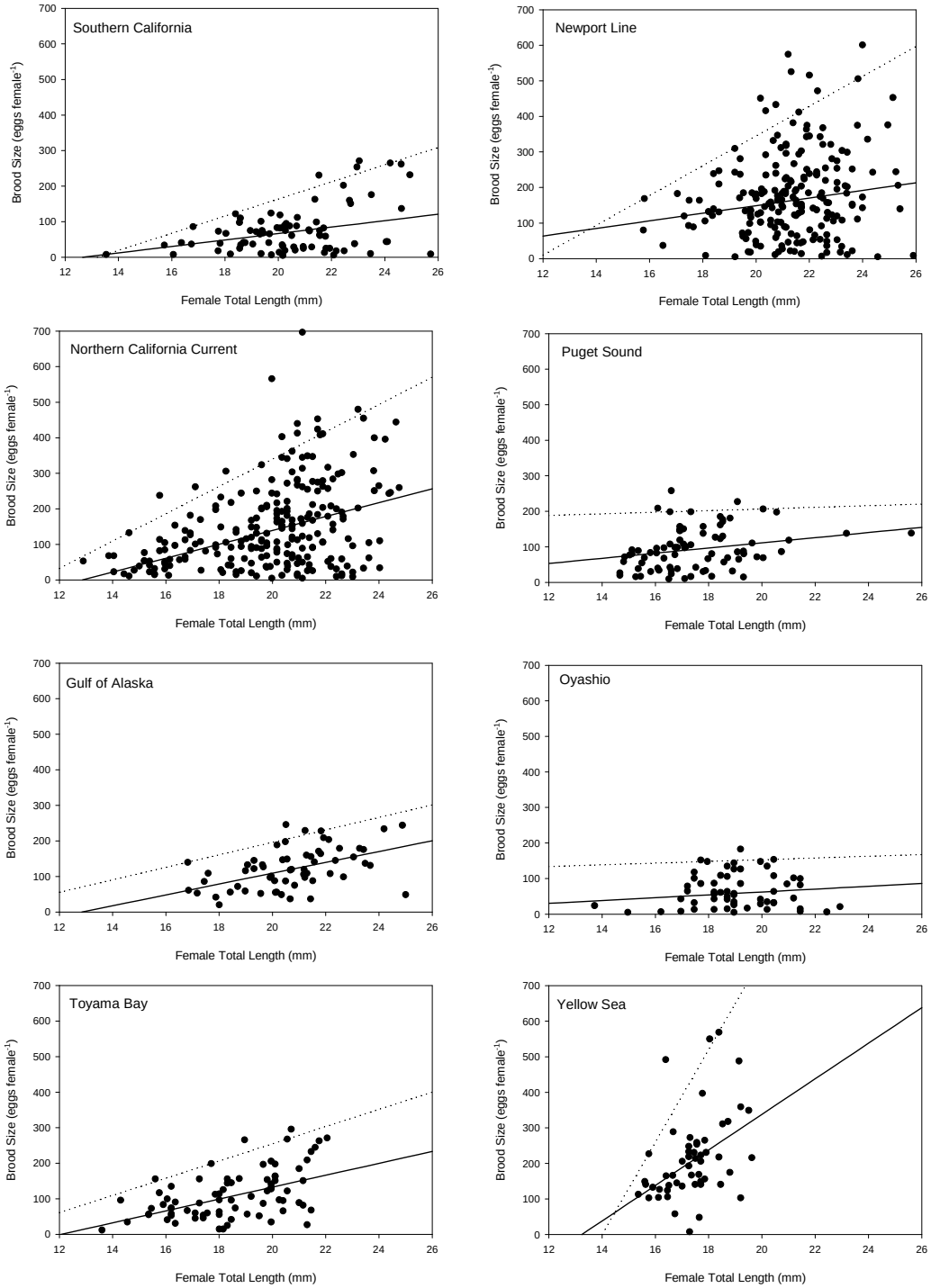

Fig. 3.6.7 *E. pacifica* total length (mm) *vs.* brood size for incubations by region. Dotted line is the estimate of the regression line for the 0.95 quantile and the solid line is the estimate for the 0.50 quantile.

Growth estimated from cohorts and molting rates

Growth rates and intermolt periods for *E. pacifica* were determined from individual growth rate (IGR) experiments carried out over a 7-year period (2000–2006) on euphausiids collected off the Oregon coast (Shaw *et al*., 2010). Adult growth rates averaged 0.020 mm total length (TL) day^{-1} during the summer upwelling season and 0.011 mm TL day^{-1}during the winter downwelling season. Average intermolt period (IMP) was 8 days during upwelling and 11 days during downwelling. Growth rates and IMPs were highly variable and were not related to surface Chl-*a* concentration or length of the euphausiid. Negative growth occurred at all times of year. Negative growth rates during winter downwelling are likely related to poor feeding conditions while negative growth rates during the summer upwelling season are likely a result of the euphausiids investing ingested energy towards reproduction rather than somatic growth. Growth rates from this study using the IGR method were generally lower than *E. pacifica* growth rates from other studies that used the cohort analysis method. Since negative growth rates are difficult to capture using cohort analysis, a seasonal growth rate was calculated using only the positive values from these experiments to compare with cohort analysis growth rates. These seasonal positive growth rates were 0.08 mm TL d^{-1} (2.4 mm month^{-1}) for the upwelling season and 0.04 mm TL d^{-1} (1.2 mm month^{-1}) for the downwelling season, equivalent to weight-specific growth rates of 0.0135 d^{-1} (upwelling) and 0.0089 d^{-1} (downwelling), and are comparable to rates obtained in other studies using cohort analysis. Highest annual growth rates during upwelling were measured in 2004 (warm) and 2006 (cold) years, suggesting that *E. pacifica* is less affected by warm and cool periods than other types of zooplankton such as copepods.

Growth rates were also estimated from cohort data from preserved samples collected at station NH25 (25 nautical miles offshore of Newport, 296 m depth) every two weeks for 11 years (2001–2011). Although *E. pacifica* spawn in this area as early as February and as late as October in association with phytoplankton blooms, there is a period of intense spawning activity in July–August which could initiate a cohort that can be followed over time. Since previous research had shown that *E. pacifica* develop from egg to juvenile in an average of 60 days (Feinberg *et al.*, 2006), a cohort that appears about two months after a spawning event could be attributed to those eggs.

There are a number of issues to consider regarding cohort analysis of euphausiids. Euphausiid distribution is notoriously patchy which may explain the disappearance and reappearance of size modes over time. Size modes may also merge as krill grow due to individual variability in development times (Feinberg *et al*., 2006). Some krill overwinter as juveniles, which can skew the timing between the appearance of eggs and the appearance of juveniles. Krill also grow more slowly at cooler temperatures and can even shrink in length under certain conditions. In addition, the winter sampling intervals were often >2 weeks due to inclement ocean conditions. The longer sampling interval, combined with potentially shrinking animals, can make it difficult to follow a cohort. In spite of all the potential difficulties, cohort analysis on this set of samples was quite successful.

Cohorts were identified using the maximum likelihood technique in MatLab. This technique identifies overlapping distributions that cannot be discerned by eye from length frequency graphs. An example of the length frequency data generated using this method indicates the presence of two size modes where the eye would distinguish only one (Fig. 3.6.8, top panel). The second and third panels (February 6 and February 14, respectively) show size modes from samples collected <2 weeks apart. Even in that short interval there was a measurable increase in each size mode. Cohort growth rates were calculated from the change in mean length of each size mode from one sampling date to the next.

Growth experiments on live krill and cohort analysis yielded similar rates (Fig. 3.6.9) but the results are not interchangeable. Both methods provide useful information about euphausiid growth, with results from cohort analysis indicating the overall population trend and results from molting rate experiments illustrating the range of individual variability. Growth rates of individual live krill (gray solid circles) show that individual variability is very high, ranging from –0.2 mm day^{-1} to 0.3 mm day^{-1}. Growth rates from cohort analysis (red diamonds) show that growth rates are higher for smaller animals and decrease as they reach their adult size. Negative growth occurs frequently for individual animals and was also identified occasionally with cohort analysis. For both methods, instances of negative growth increased after the krill reached 10 mm in length. This is the approximate length at which the krill may become reproductively

active under favorable environmental conditions. Krill that are reproductively active often shrink in length as a result of devoting energy to reproductive output instead of to somatic growth.

Feeding and metabolism

As noted previously in this report, *E. pacifica* occupy a wide range of habitats throughout the Pacific Ocean: cold upwelled waters off the Pacific Northwest, low chlorophyll regions across the North Pacific, and warm, seasonally subtropical waters off Japan, Korea, and China. The success of this species in such a wide variety of ecosystems suggests that their diets are flexible and that they are able to consume a wide range of food types and sizes. The ability to feed on small particles at low concentrations is essential for survival in oceanic waters. The morphology of the feeding basket of *E. pacifica* suggests that they are able to filter particles as small as 2 μm (Suh and Choi, 1998).

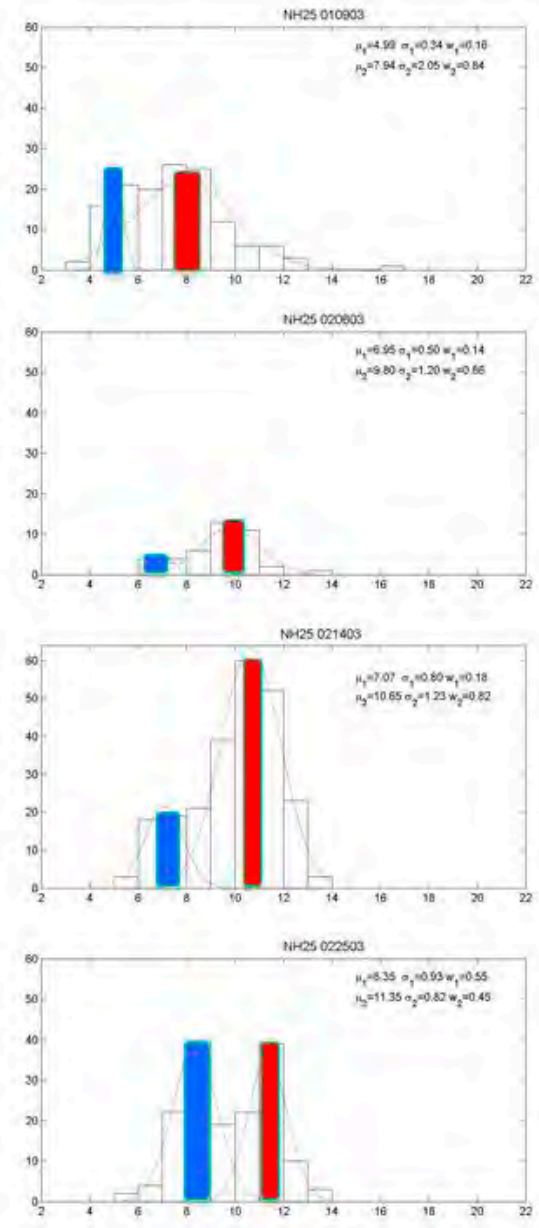

Fig. 3.6.8 Cohort data generated using the maximum likelihood method. From top, sample dates are January 9, February 6, February 14, and February 25, 2003. The colored bars designate two cohorts. Even in a 2-week interval, there is an increase in the mean length of each cohort. *x*-axis = Body length (mm), *y*-axis = Frequency.

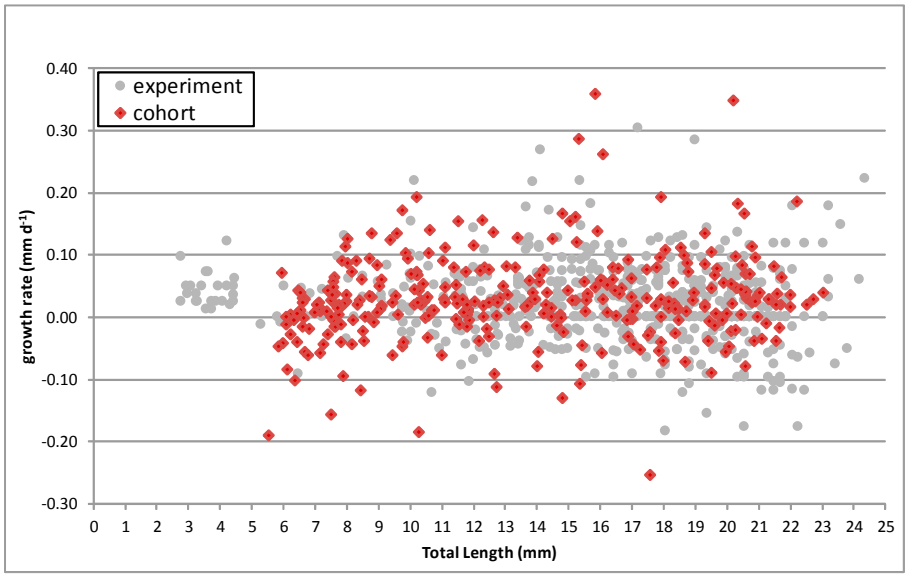

Fig. 3.6.9 Comparison of growth rates of *E. pacifica* estimated from cohort analysis (red diamonds) and from molting rate experiments on live krill (gray solid circles).

Previous studies on feeding by *E. pacifica* in comparison with results from feeding experiments by Sremba and Peterson (unpublished) are summarized in Table 3.6.1. Laboratory experiments by Sremba and Peterson using five species of cultured phytoplankton (*Chaetoceros neogracile* (CG in Fig. 3.6.10, 4.7 µm diameter), *Thalassiosira pseudonana* (3H, 4.4 µm diameter), *Isochrysis* sp. (TI, 4.6 µm diameter), *Rhodomonas salina* (3C, 7.0 µm diameter) and *Tetraselmis chui* (TC, 9.2 µm diameter) found that *E. pacifica* could feed on all of these sizes and types of small cells at rates of 100,000 to 300,000 cells h^{-1} at concentrations of ~100 µg C L^{-1} (Fig. 3.6.10). Ingestion rates varied from 1–3 µg C euphausiid^{-1} h^{-1} at low food concentrations (~50 µg C L^{-1}) to 15 µg C euphausiid^{-1} h^{-1} at high food concentrations (~800 µg C L^{-1}). Ingestion rates as a function of food concentration when fed on *R. salina* alone were similar, ranging from 2–15 µg C euphausiid^{-1} h^{-1}, or 50 to 350 µg C euphausiid^{-1} day^{-1} at the lower and higher food concentrations of ~50 and 800 µg C L^{-1}, respectively. These values are equivalent to ingestion rates of 3 to 20% of body carbon day^{-1}.

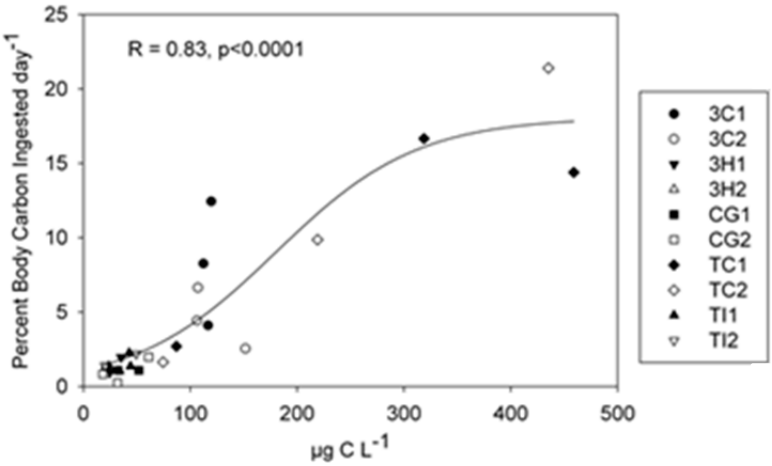

Fig. 3.6.10 Daily ration of adult female *E. pacifica* when fed various foods (described in text). Daily rations varied from a few percent per day at low food concentrations to a maximum of ~18%.

Table 3.6.1 Results of published *E. pacifica* feeding studies compared to results of Sremba and Peterson (unpublished).

Reference	Published results	Sremba and Peterson*
Parsons *et al*. (1967)	• Ingested 15% body weight day^{-1}; • grazed particles as small as 5 µm at a concentration of 131 µg C L^{-1}	• Average of 18% body weight day^{-1} at food concentrations > 400 µg C L^{-1}; • grazed particles as small as 4.4 µm
Ross (1982)	• Ingested 13% body weight day^{-1}at 8º C; • Ingested 20% body weight day^{-1}at 8º C at > 350 µg C L^{-1}	• Averaged 18% body weight day^{-1}at food concentrations > 400 µg C L^{-1}
Ohman (1984)	• Filtered 30–100 ml euph h^{-1} on *T. angstii* (33 µm diameter); • ingested 7% body carbon d^{-1} at cell concentrations of 200 µg C L^{-1}	• Filtered on average 42–44 ml euph h^{-1} at concentrations > 200 µg C L^{-1}; • 7% body carbon day^{-1} at 200 µg C L^{-1}; ~ 18% body carbon day^{-1}at 500 µg C L^{-1}
Dilling *et al.* (1998)	• Ingested 9–15 µg C euph h^{-1}; • Filtered 28–47 ml euph h^{-1} at a concentration of 200–400 µg C L^{-1}	• Ingested up to 7-10 µg C euph h^{-1}; • Filtered 42–44 ml euph h^{-1} on average
Passow and Alldredge (1999)	• Ingested 8–18 µg C mg euph C h^{-1}; • Filtered 13–75 ml euph h^{-1} at a concentration of 300–500 µg C L^{-1}	• Ingested up to 7–10 µg C euph h^{-1}; • Filtered 42–44 ml euph h^{-1} on average
Bargu *et al.* (2006)	• Ingested 1–3 × 10^{-4} cells mg h^{-1} *Pseudonitschia*	• 5 × 10^{-4} cells mg h^{-1} *Rhodomonas*

* Unpublished

To determine what the euphausiids are eating in the ocean, natural assemblage feeding experiments were conducted by Xiuning Du, a graduate student from Ocean University of China in Qingdao who worked in the Peterson lab from September 2009 to April 2011. These experiments were conducted prior to and during the upwelling season in 2010. Ingestion rates based on cell counts were highly variable, with values ranging from –0.6 to 46.3 µg C euphausiid^{-1} h^{-1} (Table 3.6.2). During the upwelling season, ingestion rates ranged from 4.8 µg C euphausiid^{-1} h^{-1} (Expt. 6) to 46.3 µg C euphausiid^{-1} h^{-1} (Expt. 9). Higher ingestion rates were related to higher food concentrations (Expts. 5, 7, 9), and comparatively lower ingestion rates were coincident with low food supply and upwelling relaxations (Expts. 6, 8). Ingestion rates based on Chl-*a* were also highly variable, ranging from 0.04 to 0.9 µg Chl-*a* euphausiid^{-1} h^{-1} during the upwelling season and from 0.01 to 0.03 µg Chl-*a* euphausiid^{-1} h^{-1} before the upwelling season was initiated. Daily ingested carbon (Daily Ration, DR) variations were in agreement with ingestion rates based on cell counts with higher values during the upwelling season (2.4~23.3%) and lower values prior to the upwelling period (0.04~1.8%).

Ingestion rates were related to food concentrations (Fig. 3.6.11), with rates of 3–5 µg C euphausiid^{-1} day^{-1} at 50 µg C L^{-1}, 15 µg C euphausiid^{-1} day^{-1} at 200 µg C L^{-1}, and a maximum of 25 µg C euphausiid^{-1} day^{-1} at 260 µg C L^{-1}. Ingestion rates increased significantly as total food biomass increased ($F = 157.06$, $P < 0.0001$, $R^2 = 0.88$).

Table 3.6.2 Euphausiid feeding experiments 2–9. Filtration rate (F ± SD), Ingestion rate (I ± SD) and Daily Ration (DR ± SD) based on microplankton cell counts, calculated carbon biomass (µg C L^{-1}), and Chl-*a* concentration (µg L^{-1}). Also shown are total length (TL) of krill in each experiment and carbon weight (wt) of krill. Note that ingestion rate for feeding on Chl-*a* is µg Chl-*a* euphausiid^{-1} h^{-1}; F = krill weight specific filtration rate (ml mg C^{-1} h^{-1}).

	F (ml euphausiid^{-1} h^{-1})		**F (ml mg C^{-1} h^{-1})**		**I (µg euphausiid^{-1} h^{-1})**		**DR (% body C d^{-1})**		
Expt. No.	**cell counts [C]**	**Chl-*a***	**cell counts [C]**	**Chl-*a***	**cell counts [C]**	**Chl-*a***	**cell counts [C]**	**TL (mm)**	**wt (mg)**
2	–30.7	8.0 ± 8.5	–10.0	2.2 ± 3.0	–0.6	0.01 ± 0.01	–0.50	17.6 ± 1.2	3.1 ± 0.6
3	6.9 ± 21.0	30.4 ± 10.3	1.8 ± 4.5	6.4 ± 2.6	0.1 ± 0.3	0.01 ± 0.003	0.04 ± 0.13	20.3 ± 1.7	4.9 ± 1.1
4	195.0 ± 35.5	97.9 ± 9.5	46.7 ± 15.9	23.1 ± 6.2	3.4 ± 0.4	0.03 ± 0.003	1.8 ± 0.4	20.1 ± 1.4	4.6 ± 1.1
5	202.8 ± 95.0	129.7 ± 20.3	39.8 ± 18.4	25.5 ± 3.8	16.1 ± 6.1	0.07 ± 0.007	7.6 ± 2.8	20.7 ± 0.8	5.1 ± 0.6
6	114.8 ± 66.2	57.8 ± 18.1	24.3 ± 11.6	12.5 ± 3.0	4.8 ± 1.8	0.04 ± 0.01	2.5 ± 0.7	19.9 ± 1.9	4.6 ± 1.3
7	101.9 ± 79.5	105.4 ± 58.8	16.6 ± 10.8	17.4 ± 7.7	14.0 ± 7.0	0.54 ± 0.18	5.6 ± 2.1	21.6 ± 1.3	5.9 ± 1.0
8	135.4 ± 34.5	167.9 ± 43.5	21.7 ± 5.9	27.0 ± 7.2	6.1 ± 0.5	0.26 ± 0.03	2.4 ± 0.2	22.1 ± 1.5	6.3 ± 1.3
9	78.3 ± 30.1	52.8 ± 14.0	17.6 ± 9.3	12.2 ± 5.6	46.3 ± 22.0	0.90 ± 0.18	23.3 ± 16.6	20.8 ± 2.7	5.4 ± 2.3

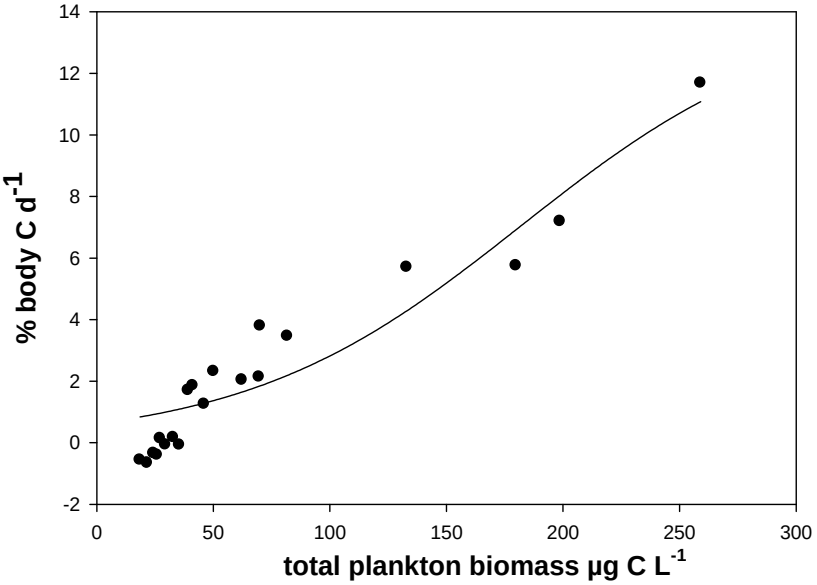

Fig. 3.6.11 Daily ration in percent body carbon consumed per day, for all experiments. Note the similarity to the results of the Sremba and Peterson experiments (Fig. 3.6.10).

Feeding selectivity

Data from the natural assemblage feeding experiments can also determine whether *E. pacifica* have a preference for certain food types. During the experimental period, the microplankton community structure showed obvious seasonality, with diatoms dominant during bloom periods and small flagellates, ciliates, or dinoflagellates dominant during other periods. Krill seem to adapt to ambient food conditions by feeding on whatever is available when food supplies are low but feeding selectively when given the opportunity.

When ciliates dominated the total biomass they were a preferred prey item. Small flagellates (5~20 µm) and silicoflagellates were also positively selected under these conditions. When a variety of diatoms were available, *E. pacifica* fed preferentially on *Pseudo-nitzschia* spp., *Leptocylindrus* spp., *Chaetoceros* spp., *Coscinodiscus* spp., *Asterionellopsis glacialis*, and *Thalassiosira* spp., as well as small flagellates and silicoflagellates. Under these conditions the krill appeared to avoid dominant dinoflagellates such as small dinoflagellates and *Heterocapsa triquetra* as well as tintinnids and naked ciliates.

Some prey items were clearly preferred even when they were not the dominant prey available. Krill kept their strong preference for the far less dominant diatoms such as *Asterionellopsis glacialis*, *Cylindro-theca closterium*, *Pseudo-nitzschia* spp., and *Lepto-cylindrus* spp. Under these conditions, they also preferred the dominant *Dinophysis* spp., naked ciliates (>40 µm) and tintinnids in comparison with other dominant prey items such as naked ciliates (<40 µm), *Protoperidinium* spp., and small flagellates.

When the prey field was dominated by diatoms (Table 3.6.2, Expt. 7) krill showed a strong preference for the dominant diatom *Chaetoceros* spp. as well as less dominant diatoms such as *Eucampia zodiacus*, *Guinardia delicatula*, *Pseudo-nitzschia* spp., *Skeletonema* spp. and *Thalassiosira* spp. Krill appeared to avoid some dominant diatoms such as *Lauderia annulata* and *Leptocylindrus* spp., as well as naked ciliates. However, in other experiments where diatoms were dominant (Expts. 8, 9), krill seemed to avoid the abundant diatom *Chaetoceros* spp. which they had preferred during the previous experiment. Instead, they preferred less dominant diatoms such as *Lauderia annulata*, *Leptocylindrus* spp., *Pseudo-nitzschia* spp., *Skeletonema* spp., *Thalassiosira* spp., as well as ciliates.

In general, *E. pacifica* fed preferentially on large dominant phytoplankton over smaller cells (flagellates) and always fed on ciliates when they were present regardless of whether phytoplankton

were abundant or not. *E. pacifica* showed strong selectivity for diatoms, although they did not always feed preferentially on the dominant species of diatom. Diatoms were selected over other food types, even ciliates, during the upwelling bloom period. There was no evidence of a preference for dinoflagellates. These results suggest that *E. pacifica* feed preferentially on diatoms and ciliates when they have the option. When they don't, *E. pacifica* will feed on whatever is available. This flexibility in diet contributes to their ability to survive in the wide variety of habitats they occupy throughout the North Pacific.

Other research has shown that *E. pacifica* consumes protozoans like ciliates and tintinnids (*e.g.*, Nakagawa *et al*., 2001; Nakagawa *et al*., 2004). Nakagawa *et al*. (2002) found that heterotrophic prey accounted for 57–79% of total ingested carbon (54–77% from copepods) in May and for 27–93% of total ingested carbon (27–93% copepods) in October. Ohman (1984) found that *E. pacifica* in Dabob Bay, Puget Sound, Washington, consumed some *Pseudocalanus* sp., though they were considered a suboptimal food source compared to diatoms.

Studies of copepods that exhibit diel vertical migration generally show empty or near empty guts during the day at depth and high feeding activity at night near the surface. In contrast, studies suggest that vertically migrating euphausiids continue to feed at depth during the day. Several studies on different species of vertically migrating euphausiids have found evidence of this feeding strategy. Nakagawa *et al.* (2003), working in waters off northeastern Japan, found that *E. pacifica* gut contents were predominantly phytoplankton at night when the euphausiids were feeding near the surface. During the day when the euphausiids were feeding at depth, they found copepods and tintinnids in the guts. Schmidt (2010) found that *Meganyctiphanes norvegica* fed on phytoplankton at the surface at night and fed on copepods and sinking detritus at depth during the day. Stuart and Pillar (1990), working in the southern Benguela Current, found that *Euphausia lucens* fed carnivorously at depth during the day. Hamame and Antezana (2010) found that euphausiids (not *E. pacifica*) in the fjords of southern Chile fed on phytoplankton near the surface at night and on benthic polychaetes during the day at shallow stations. Copepods were also more frequently a part of the daytime diet.

Feeding by *E. pacifica* is highly opportunistic, adaptive, and flexible and this contributes to its success as a species. In contrast with findings from studies of copepods, diel vertical migration does not preclude 24 hour feeding by euphausiids. Their diet changes from phytoplankton at night when feeding in surface waters, to protozoa and copepods during the day when feeding at depth, and possibly even benthos if the daytime is spent near the bottom. The ability to feed on a wide variety of prey types – phytoplankton, microzooplankton, mesozooplankton, marine snow, phytodetritus, and perhaps benthos over a broad range of sizes (2 μm phytoplankton to copepods that are several mm in length) and particle concentrations must certainly contribute to the success of *E. pacifica* in the wide range of different environmental conditions it inhabits.

3.6.7 Lipid Analysis

Off Oregon, *E. pacifica* lipid reserves showed only minor seasonal variations (5–20%, Fig. 3.6.12, Ju *et al*., 2009). This suggests that *E. pacifica* are not accumulating stored lipids as food reserves but are allocating energy to growth and reproduction. *E. pacifica* spawning is closely tied to the timing of phytoplankton blooms off Oregon, suggesting that this species can maintain itself on a diet of ciliates, copepods, marine snow, *etc*., but needs the concentrated pulse of high quality food provided by phytoplankton blooms to fuel reproductive activity.

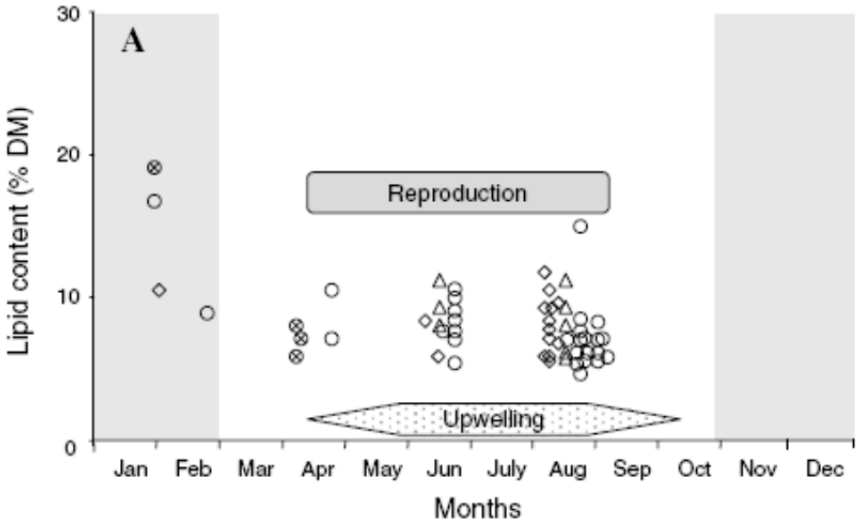

Fig. 3.6.12 Seasonal variations in lipid content of *E. pacifica* from animals collected off the Oregon coast (from Ju *et al.*, 2009). Diamond = furcilia, triangle = juvenile, circle = adult.

3.6.8 Carbon:Nitrogen (C:N) Analysis

C:N analysis has been conducted for *Euphausia pacifica* and *Thysanoessa spinifera* juveniles and adults collected off Newport. C:N ratios were distinctly different between these two species, possibly reflecting different levels of lipid content (Fig. 3.6.13). C:N ratios of *E. pacifica* (~7–21 mm) were constant over this size range, averaging 4.4. C:N ratios for *T. spinifera* (~8–25 mm) were generally higher than for *E. pacifica*, were far more variable, and have a higher average (C:N = 5.8). Since *T. spinifera* reach sexual maturity at a body length of ~ 12 mm, and since it is at this length that C:N begins to increase, this suggests that the change in C:N ratio is related to reproduction. C:N ratios may be highest in females with lipid-rich eggs in their ovaries. Future goals are to test this hypothesis by analyzing lipid content of the animals by sex, maturity stage, and level of ovarian development.

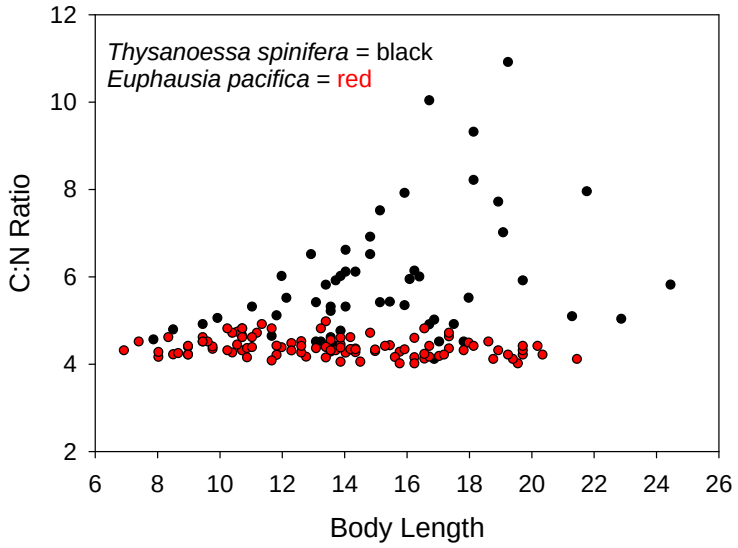

Fig. 3.6.13 C:N ratios of euphausiids collected along the Newport Hydrographic Line. Body length in mm.

3.6.9 Population Genetics

The pan-Pacific distribution of *E. pacifica* has led to speculation about whether *E. pacifica* in specific geographic locations constitute distinct populations or whether this species can be considered one population throughout its range. Population structure can be measured through the comparison of genetic diversity between populations. The Peterson lab conducted the first steps in this process by identifying regions of variability within the nuclear and mitochondrial genome in order to develop the tools to measure genetic diversity within populations. We identified regions of variability in the mitochondrial genomes of several euphausiid species (*E. pacifica*, *Thysanoessa raschii* and *E. superba)* and developed microsatellites within the nuclear genome of *E. pacifica*.

To date, we have sequenced near-complete mitochondrial genomes for *E. pacifica* and *T. raschii* (Johansson *et al.*, 2012a) as well as five mitochondrial genomes of *E. superba* (Johansson *et al.*, 2012b) using 454 next generation sequencing. Based on these data we were able to identify regions of high variability within the mitochondrial genome of all three species. For example, comparisons between Bering Sea and Yellow Sea *E. pacifica* revealed a total of 644 variable sites. These regions of variability within the mitochondrial genome can be targeted to describe the genetic diversity within a population for comparison to other populations. Future genetic analyses can concentrate on these regions of high variability since genetic differences are likely to be found at these locations. Phylogenetic analyses to assess the phylogenetic position of the Euphausiacea, using the concatenated nucleic acid sequences of *E. pacifica* and *T. raschii*, along with 46 previously published malacostracan mitogenomes, support the monophyly of the order Decapoda and indicate that the Euphausiacea share a common ancestor with the Decapoda (Johansson, 2012b). Other recently published research conducted in China also found a close relationship between Euphausiacea and Decapoda and suggested a close relationship between Euphausiacea and Penaeidae (Shen *et al.*, 2011).

We also developed five microsatellite markers for *E. pacifica* using the next-generation sequencing based technique developed by Abdelkrim *et al.* (2009). DNA was enriched for microsatellite repeats at the Savannah River Ecological Laboratory and the enriched library was sequenced using 454 next generation sequencing. Microsatellite repeats were identified and primers were designed using MsatCommander (Faircloth, 2008). Primers were tested for 41 microsatellite loci and five microsatellites amplified successfully. Twenty individual *E. pacifica* from each of four collection sites (Oregon coast, Bering Sea, Gulf of Alaska, and Yellow Sea) were screened for five microsatellite loci. The Peterson lab intends to submit a primer note to the journal Molecular Ecology Resources with our results, including basic statistics (number of alleles at each locus, observed and expected heterozygosities, and polymorphism) and tests for deviation from Hardy-Weinberg equilibrium and linkage disequilibrium.

These markers provide tools to explore the population structure of *E. pacifica* throughout the North Pacific. Continued genetic analyses of *E. pacifica* across the North Pacific will provide evidence of the evolutionary history of this species and the potential to detect underlying population structure and adaption throughout the region.

4 Euphausiids in North Pacific Continuous Plankton Recorder Sampling

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4.1 Background

Euphausiids are one of the more common taxa caught by the Continuous Plankton Recorder (CPR), although the largest individuals are probably too large to pass through the aperture in the nose cone (which is a square with 1.27 cm sides). The ability of the CPR to catch euphausiids has not been investigated in any detail although Glover (1962) suggests that despite the small aperture, the CPR catches large, active organisms such as euphausiids perhaps better than a slow-moving net because of the high sampling speed and the absence of a bridle in front of the aperture. An additional issue, however, is that the CPR is towed at a fixed, near-surface depth (~7 m) and because most euphausiids migrate closer to the surface at night and/or are less able to avoid the CPR at night, abundances in nighttime samples are generally much higher. Nevertheless, CPR data have been used to describe the population dynamics of euphausiids in the past (Lindley and Williams, 1980) and in a study based on CPR samples in the early years of the North Pacific CPR survey the known range of one euphausiid species, *Thysanoessa inspinata*, was extended (Lindley *et al*., 2004). Euphausiids are not routinely identified to species in ordinary CPR sample analysis; the sampler is quite hard on organisms and damage is frequent, making identification time-consuming. However, accomplished analysts could identify the majority of specimens. The full range of species sampled is, therefore, not known at this time; however, the following have been positively identified from the NE Pacific; *Thysanoessa inermis, T. longipes, T. inspinata, T. spinifera, T. rachii* and *Euphausia pacifica.*

Data from the North Pacific CPR survey were examined to determine basic seasonal and interannual variability across the region, as a contribution to the PICES WG 23 final report.

4.2 North Pacific CPR Data

Full details of CPR sampling can be found in Batten *et al.* (2003), but essentially the device is towed behind commercial ships at a fixed depth of about 7 m. There are two transects operating in the NE Pacific; one north–south which is towed about 6 times per year between the western coast of North America and Alaska and one east–west transect which is towed 3 times per year between North America and Japan. Seawater enters the front of the machine as it is pulled through the water and plankton are filtered onto a continuously moving band of filtering mesh, with a mesh size of 270 µm. The mesh is wound into a storage tank containing formaldehyde which fixes and preserves the plankton. Once back in the laboratory, the mesh is cut into discrete samples, based on the ship's log information, each representing 18 km of tow, and about 3 m^3 of seawater. The midpoint of each sample is allocated a position, time and date based on the log information. Every fourth sample is analysed microscopically and individuals are identified and counted. Remaining samples are archived. Euphausiid eggs, nauplii and calyptopis stages are counted in a subsample (about 1/50 of the sample) while large sub-adults and adults are counted from the whole sample.

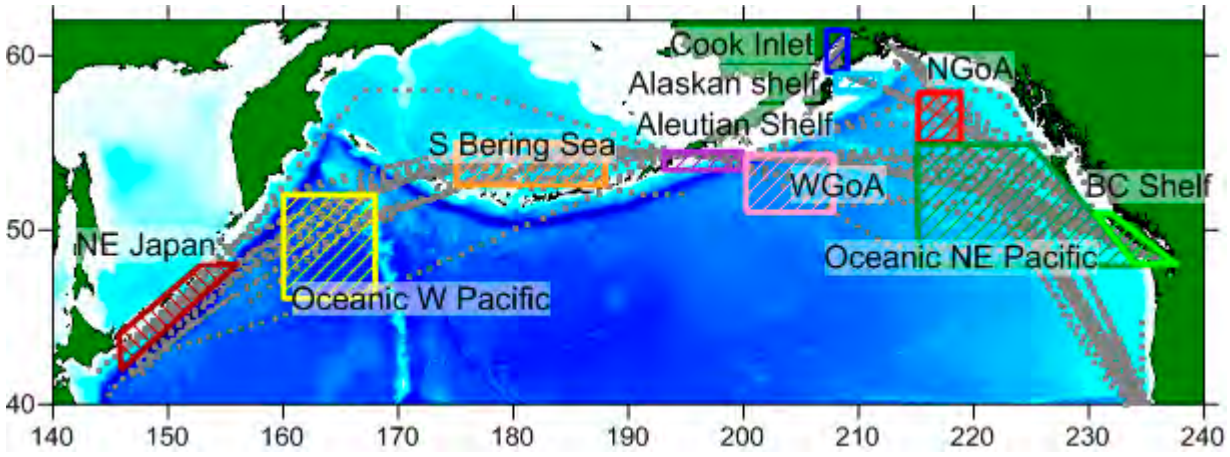


Fig. 4.2.1 Location of CPR samples (grey dots) collected and analysed, 2000 to 2012. Note that at the time of this writing, the abundance data for 2012 has not been quality controlled and finalized, so only samples up to 2011 have been discussed in the text. Midpoints of the 18 km samples are allocated a latitude (°N) and longitude (°E). Sub-regions used in this report are overlaid. GoA = Gulf of Alaska, BC = British Columbia.

Of the 4,922 processed CPR samples collected from 2000 to 2011, 2,527 samples contained euphausiids, a little over 51%. Sub-regions of the sampled area have been previously defined and are used here (Fig. 4.2.1). These regions are hydro-dynamically distinct, *e.g.*, shelf *versus* oceanic, and span the geographic range of the survey. Figure 4.2.1 shows the location of CPR sampling of the North Pacific and the sub-regions used in this report.

4.2.1 Seasonal Cycles

Euphausiids are more abundant in CPR samples at night because of diel vertical migration and likely lower avoidance of the sampler; however, not all regions were sampled equally intensively by day and night. There are more daytime samples because the CPR samples are collected between spring and fall and at these subarctic latitudes during this timeframe there is more daylight than dark. Mean seasonal cycles of adults are shown in Figure 4.2.2. Where sampling was sufficiently frequent (>4 samples in that month) both day and night samples are used to calculate two separate monthly averages, otherwise, just daytime sample averages are shown. Note that the sample processing of Western Pacific samples was taken over by Japanese colleagues after 2009 so the data shown here for the Oceanic Western Pacific and NE Japan regions are from 2000–2008 only.

The Aleutian shelf region containing Unimak Pass had the highest number of euphausiids, day or night, of all the regions and, in fact, observations of the filtering mesh while unloading the CPR have often predicted where the Aleutian shelf was crossed because of the density of euphausiids clearly visible on the mesh. Both day and night data suggest an increase in numbers through the spring and summer, reaching a peak in late summer. This pattern is similar off the shelf immediately to the east (Western Gulf of Alaska region) and west (Southern Bering Sea region). The seasonal cycle farther east appears earlier, with a peak in June in the oceanic region and Northern Gulf of Alaska. Abundances on the northern shelf, in Cook Inlet and the Alaska shelf regions are low, though this is likely because nighttime samples were too rare to include. The seasonal cycle, again, is earlier with a peak in spring in Cook Inlet and summer on the open Alaskan shelf. Not enough months were adequately sampled in the Western Pacific to be clear on the seasonal cycle but it appears to be late summer that sees the highest numbers.

Juvenile euphausiid stages are less common and less abundant in CPR samples. This is likely related to depth of sampling with respect to the depth of the organisms. The seasonal cycles are not well defined for most regions and so data are not included here (but are available on request).

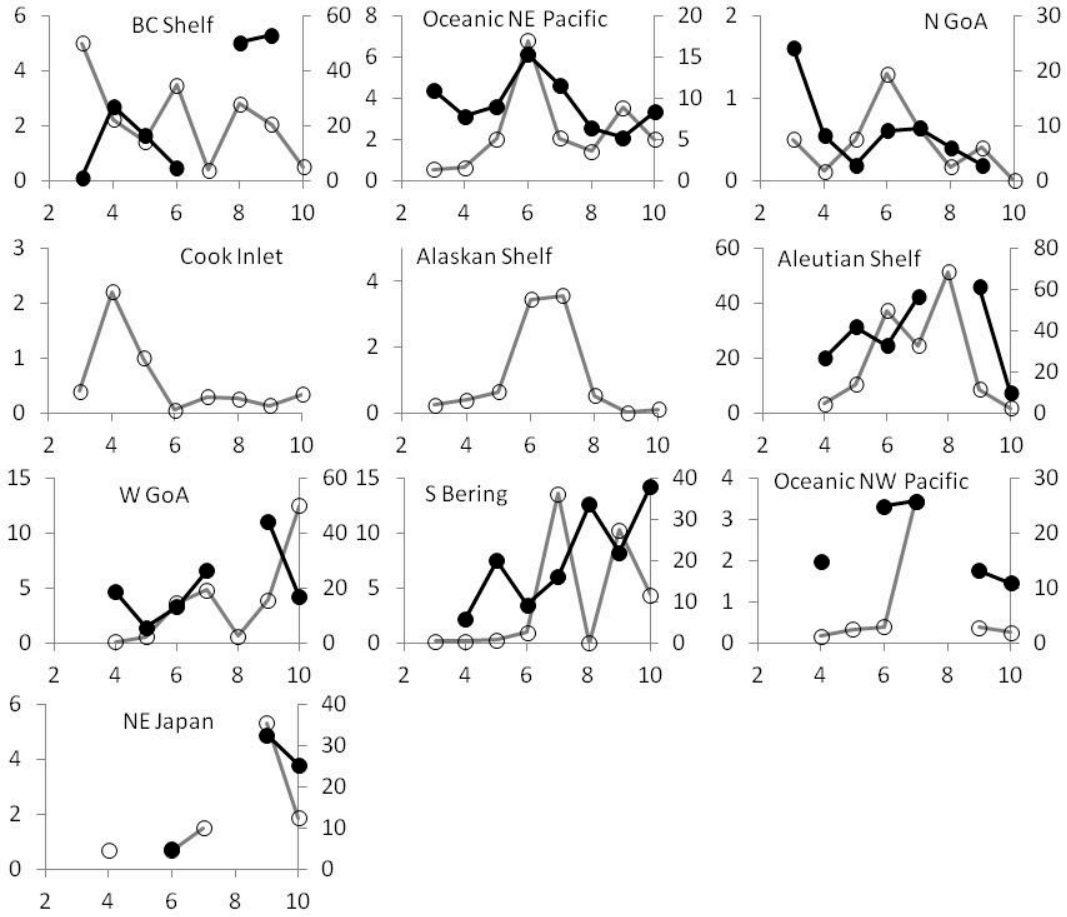


Fig. 4.2.2 Mean monthly abundance of adult and sub-adult euphausiids for each region sampled by the CPR. Abundances are expressed as numbers per CPR sample (typically 3 m^3). Filled circles and black lines = night (righthand axis), open circles and grey lines = day (lefthand axis); *x* axis = month.

4.2.2 Interannual Variability

Not all months in all years were sampled for any region, owing to last minute schedule changes by the ships, or mechanical failure of the CPR, which makes calculation of a realistic annual mean problematic. Furthermore, regions to the east that were sampled by the north–south transect were sampled normally at least 5 times per year, while regions to the west only sampled by the east–west transect were sampled, at best, 3 times per year.

Gaps in the time series for eastern regions were filled according to the following formula for the months April to September, inclusive:

(monthly mean for that month × annual mean for that year)/overall monthly mean

For regions to the west, a simple summer mean was calculated since this season was sampled each year from 2000 to 2011. Daytime samples only were used except for the Northern Gulf of Alaska region, which was most often sampled by night, where nighttime samples were used. Resulting time series are shown in Figure 4.2.3.

No region has a significant linear trend over the whole time series, though the Oceanic NE Pacific region (which has the greatest sampling intensity) shows a declining trend from 2006 to 2011.

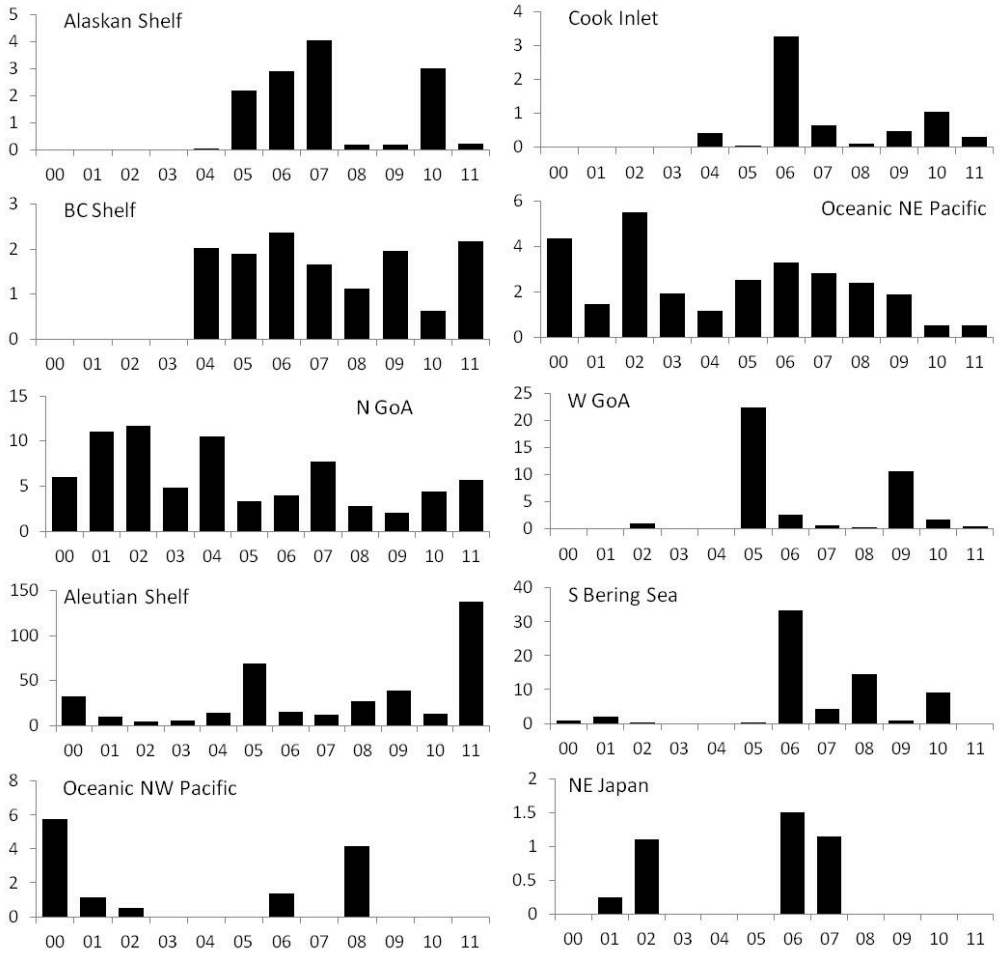


Fig. 4.2.3 Mean annual abundance of adult euphausiids per region (see text for derivation and note that abundances cannot be compared between regions as method of derivation varies between regions). *y* axis = numbers per sample, *x* axis = year. Region descriptions are given in Figure 4.2.1.

Interestingly, all the regions to the east of the Aleutian Islands have a positive correlation with the annual mean Pacific Decadal Oscillation (PDO) while regions west of and including the Aleutian Islands have a negative correlation. None of these correlations are significant at $p < 0.05$. However, it suggests that there is an element of climate forcing in the interannual variability shown here, given that the PDO has an opposing expression in the eastern and western ocean Pacific basins; when positive, the eastern NE Pacific tends to be warm while the west is cool, and *vice versa* (see Batten *et al*. (2010) for further information on climate indices). This relationship warrants further examination as the times series develops.

In conclusion, the CPR survey can provide broad scale information on euphausiids across the PICES region and such data will continue to be collected. In addition, there is a large sample archive available (over 12,000 samples) that researchers can use for additional studies. Anyone interested in further data or samples should contact the author of this section.

Acknowledgements

Pacific CPR data collection is supported by a consortium for the North Pacific CPR survey coordinated by the North Pacific Marine Science Organization (PICES) and comprising the North Pacific Research Board (NPRB), Exxon Valdez Oil Spill Trustee Council (EVOS TC), Canadian Department of Fisheries and Oceans (DFO) and the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). The efforts of the volunteer vessels that tow the CPRs, their officers, crew and port staff, are gratefully acknowledged.

5 Modeling

Modeling activities within the krill Working Group were conducted by Dr. Michio Kishi (WG 23 member) and Dr. Harold (Hal) Batchelder, using the NEMURO (**N**orth Pacific **E**cosystem **M**odel for **U**nderstanding **R**egional **O**ceanography) model (Kishi) and Individual-Based Modeling (IBM, Batchelder).

5.1 NEMURO Model

Aita *et al.* (2003) first showed the results of NEMURO (Kishi *et al.*, 2007a,b) embedded in a three-dimensional ocean physical model and pointed out the importance of vertical migration of copepods in the Northern Pacific, which was also identified by Kishi *et al.* (2001). NEMURO contains a compartment for predatory zooplankton (ZP), which includes jellyfish, krill, and other higher trophic animals. Different life stages of krill are not incorporated into NEMURO; however, there are some continuous modeling efforts being done on copepods related to NEMURO. Terui and Kishi (2008) modified NEMURO by adding population dynamics of a copepod (*Neocalanus cristatus*), and Terui *et al.* (2013) added a Lagrangian ensemble model of it. These models reveal the behavior of *Neocalanus* and their role in relation to lower trophic levels of the ecosystem in the northwestern Pacific. Efforts toward modeling krill in the northwestern Pacific are still ongoing. As shown in Kishi *et al.* (2009) and Kishi *et al.* (2010), the output of ZP from the NEMURO model can be useful as an indicator of prey for chum salmon or Pacific squid. The results obtained thus far suggest that the initial NEMURO model provides a good representation of conditions in the northwestern Pacific.

5.2 Individual-Based Models and Bio-physical Models

Modeling of cross-shelf transport in the Oregon upwelling zone was done by Dr. Hal Batchelder and his Ph.D. student, Brie Lindsey. The initial goals of these efforts were to (1) model the population dynamics of *Euphausia pacifica*, including birth and death rates, growth rates, and secondary production, and (2) investigate mechanisms of transport, retention, and loss of euphausiids in the Oregon upwelling system using coupled bio-physical and individual based models. Results from their effort to develop the coupled bio-physical models to investigate the role of transport in controlling retention and loss are reported below and in Lindsey and Batchelder (2011). Modeling of the population dynamics is still ongoing.

The Oregon coast is characterized by a summer upwelling season with frequent upwelling-favorable wind events interspersed with relaxation of the winds. The resulting offshore movement of surface waters may make exploitation of the favorable nearshore environment a challenge for young, non-migratory euphausiid life stages that reside in the strongest offshore surface flows, while older life stages that engage in diel vertical migration spend more time deeper in the water column and are transported offshore at a slower rate or even remain nearshore. Lindsey and Batchelder postulated that the ratios of migrating life stages to non-migrating life stages of *E. pacifica* will reflect differential transport of these life stages and result in specific patterns of this ratio as a function of recent winds and distance offshore. The initial attempts were based on this metric, the ratio of migrating to non-migrating stages ($R_{M:N}$),

$$R_{M:N} = \log_{10}\left[\frac{a_M}{a_N}\right],$$

where a_M, the sum of abundances of all migrating stages (individuals m^{-3}) and a_N, the sum of abundances of all non-migrating stages in a given sample (individuals m^{-3}). The ratio, $R_{M:N}$, has a value of zero when $a_M = a_N$, *e.g.*, when the migrating and non-migrating larval krill abundances are equal. However, when a_N is zero (*e.g.*, there are no non-migrating stages in a sample), this metric is undefined even though zero abundance of non-migrators may be a valid estimate of field density. Consequently, Lindsey and Batchelder modified their metric to the following R_M,

$$R_M = \left[\frac{\log_{10}(a_M + 1)}{\log_{10}(a_N + 1) + \log_{10}(a_M + 1)} \right],$$

where

$$a_M = \sum_{i=11}^{14} a_i,$$

$$a_N = \sum_{i=2}^{5} a_i$$

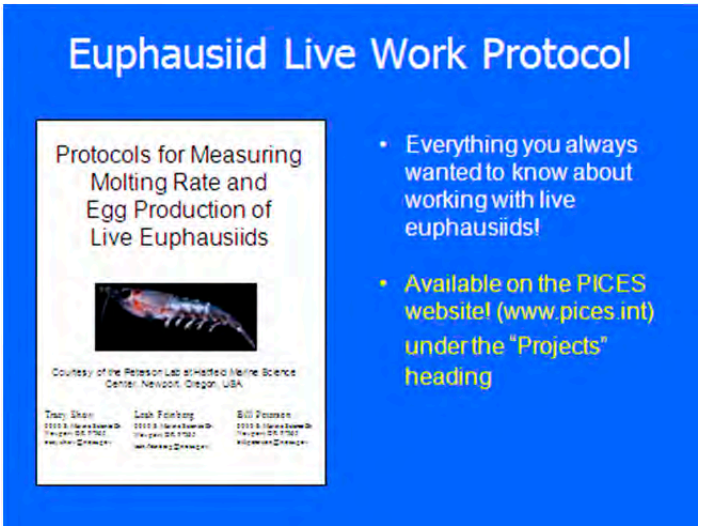
and where i indicates the life stage (1 = egg, 2 = Nauplius-1, *etc*.), and i = 2–5 represents the summed abundances of the non-migratory stages: nauplii (2 stages), metanauplius (1 stage) and first calyptopis stage, and i = 11–14 represents the summed abundances of the migratory furcilia (F4–F7) stages. The range of this sample statistic is 0.0 (only non-migrators present) to 1.0 (only migrators present). Examination of this statistic for samples having different recent (1–2 days previous) wind histories of upwelling *vs*. non-upwelling, and for inshore and offshore stations sampled on the same day (thereby having identical wind histories) provide evidence of differential cross-shelf advection of migrating *vs*. non-migrating stages of *E. pacifica*.

Lindsey and Batchelder (2011) found that cross-shelf trends in abundance were not always consistent, either in the model or in the data. What seemed at first a straightforward and testable idea (that ontogenic diel vertical migration serves to retain zooplankton in upwelling zones) was difficult to test with the physical model because of confounding interactions of time- and location-dependent spawning and strong alongshore (and potentially cross-isobath) transport driven by wind-forced Ekman transport. They found the question was more complex than envisaged because it involves not only cross-shelf data, but also knowledge of alongshore transport, stage-specific development times, individual variability in behavior, and ultimately spawning locations upstream of the sampling locations.

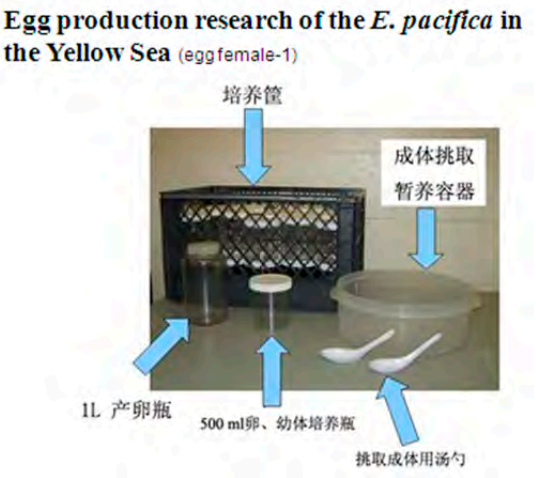
6 Other WG 23 Activities

6.1 Euphausiid Live Work Protocol

The protocols used by the Peterson lab for measurement of euphausiid molting rates and brood sizes were published to the PICES website in 2005 to assist other euphausiid researchers with incorporating these types of experiments into their existing research programs. Using consistent methods among projects generates data that are comparable among regions. Data from Japan and Korea from experiments using this protocol are included in the pan-Pacific brood size comparison paper by Feinberg *et al.* (Journal of Plankton Research, in press July 2013).



Shaw, C.T., Feinberg, L.R. and Peterson W.T. 2005. Protocols for measuring molting rate and egg production of live euphausiids. http://www.pices.int/projects/Euphasiid/euphasiid.aspx.



An illustration (left) from the Euphausiid Live Work Protocol (http://www.pices.int/projects/Euphasiid/euphasiid.aspx) showing supplies for euphausiid incubations with the names of the items translated into Chinese by the scientists who conducted live euphausiid experiments on research cruises in China.

6.2 Zotero Publications Database

In partial fulfillment of the terms of reference for WG 23, members worked towards making krill-related publications more readily available (see Other Publications on the WG 23 webpage, http://www.pices.int/members/working_groups/Disbanded_working_groups/wg23.aspx). In particular, they focused on publications that were not readily accessible electronically and papers that were originally published in a language other than English. Publications that were not easily available online included older publications, publications that appeared in the form of a technical report or institutional publication, and those published in journals that had limited electronic access (for example, that might only be accessible within certain countries). For papers that were originally published in a language other than English, the goal was to identify these papers and post partial translations – methods, results, figure captions and table legends. Toward this end, the group used the online bibliographic resource called Zotero to create a WG 23 krill library. Zotero groups allow researchers to:

- Share their own work or sources they have discovered with others who are working in related areas;
- Collaborate with colleagues, publicly or privately, on ongoing research;
- Discover other people with similar interests and the sources they are citing.

For those who are familiar with the EndNote program, Zotero also works in a similar fashion to create bibliographies. Zotero is free and registering for an account is easy and will not add you to any mailing lists. However, you do not need a Zotero account to view the WG 23 library at https://www.zotero.org/groups/pices_wg-23. When you create an account and join the group you will be able to add references to the library and use Zotero to autoformat your bibliography when writing papers.

6.3 International Collaborations

6.3.1 Visiting Scientists

Xiuning Du
Ocean University of China, Qingdao

Xiuning Du worked in the Peterson lab in Newport, Oregon, USA, from September 2009 to April 2011. She conducted experiments on feeding rates and preferences of *Euphausia pacifica*, which yielded new and interesting data on dietary preferences of the species when feeding on natural assemblages. This research comprised a substantial portion of her Ph.D. thesis. Xiuning Du was honored at PICES-2010 in Portland, Oregon, with the "Best Oral Presentation" award in a BIO-sponsored Topic Session. She also wrote and submitted a paper on harmful algal blooms off the Oregon/Washington coast using archived samples from the Peterson lab. She completed her Ph.D. in December 2011.

Ramiro Riquelme-Bugueño
Universidad de Concepción, Chile

Ramiro Riquelme-Bugueño conducted research in the Peterson lab during the summer of 2011. The lab in Concepción, Chile was severely damaged by a tsunami in February 2010 so this visit provided him with an opportunity to conduct experiments on live euphausiids. The collaboration explored using measurements of the euphausiid hepatopancreas as an indicator of physiological condition. He completed his Ph.D. in January 2012.

Nelly Tremblay
Alfred Wegener Institute, Bremerhaven, Germany

Nelly Tremblay visited the Peterson lab in September 2011 and April 2012 to conduct experiments on the effects of hypoxia on live euphausiids as part of her Ph.D. research. Her project consists of conducting hypoxia experiments on euphausiids from several different geographic locations during two seasons each. She returned to her lab in Germany with over 500 frozen samples from each of her visits to the Peterson lab. She is currently in the process of analyzing these samples and expects to complete her Ph.D. by 2014.

Dr. Toru Kobari
Kagoshima University, Japan

Dr. Toru Kobari spent four months of his sabbatical working in the Peterson lab from June to September 2012. He conducted extensive experiments on live euphausiids and copepods to analyze various methods of determining zooplankton production using biochemical assays (nucleic acids ratio, AARS, chitobiase, *etc.*). These samples are currently being analyzed in his lab at Kagoshima University in Japan. Dr. Kobari also expects to submit a proposal to PICES to establish a working group on zooplankton production.

6.3.2 Laboratory Visits

Dr. Bill Peterson spent two weeks in Qingdao, China in December 2011, attending the Ph.D. defense of Ms. Xiuning Du and presenting seminars at each of the four oceanographic institutes in Qingdao. During this visit, Dr. Peterson was appointed to an Adjunct Professorship at Ocean University of China by Prof. Quangxing Lu. Dr. Peterson visited Qingdao for a week in May 2012 to collaborate with WG 23 Co-Chairman, Prof. Song Sun, on the preparation of this report.

6.3.3 Collaborative Sampling

Tracy Shaw (WG 23 member, USA) was invited by Dr. Se-Jong Ju (WG 23 member from Korea) to participate in a Yellow Sea research cruise in August 2011 on the Korean research vessel R/V *Eardo*. She was subsequently invited back for cruises in April of 2012 and 2013. During these cruises, she and members of Dr. Ju's staff conducted experiments on live *E. pacifica* to measure growth, egg production, and feeding, and collected *E. pacifica* specimens for lipid and biochemical analyses.

Dr. Peterson (WG 23 member, USA) acquired funding to conduct some preliminary work on the population genetics structure of *E. pacifica*. WG 23 members were instrumental in obtaining *E. pacifica* specimens from around the North Pacific in order to compare individuals from a variety of geographic locations. In addition to samples collected by the Peterson lab off of Oregon, *E. pacifica* specimens for comparison were collected in the Oyashio region of Japan by Dr. Yuji Okazaki (WG 23 member), from the Yellow Sea by Dr. Se-Jong Ju, and from the Bering Sea by Tracy Shaw (as part of the BEST project).

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Appendix 2

Euphausiid Length Conversion Equations

There are many different methods of measuring the length of euphausiids. These equations allow for conversion of lengths among the more common protocols.

Equation type	Life stages	Equation	# indiv.	Size range (mm)	r^2	Source
		E. pacifica				
BL from TL	Adult	BL = 0.8237 * (TL) - 0.2924	836	TL=11.4-28.0	0.98	1
BL from TL	Juvenile	BL = 0.8294 * (TL) - 0.3089	326	TL=3.8-16.8	0.99	1
BL from TL	Furcilia	BL = 0.7954 * (TL) - 0.1279	1480	TL=1.8-10.0	0.99	1
BL from TL	Furcilia to Adult	BL = 0.8201 * (TL) - 0.2217	2642	TL=1.8-28.0	1.00	1
TL from BL	Adult	TL = 1.1954 * (BL) + 0.6548	836	BL=9.0-23.2	0.98	1
TL from BL	Juvenile	TL = 1.1894 * (BL) + 0.4543	326	BL=3.0-13.5	0.99	1
TL from BL	Furcilia	TL = 1.2468 * (BL) + 0.1889	1480	BL=1.3-7.7	0.99	1
TL from BL	Furcilia to Adult	TL = 1.218 * (BL) + 0.2807	2642	BL=1.3-26.0	1.00	1
CL from UL	Juvenile-Adult	CL = 1.48 * (UL) + 0.25	340	TL=3.0-20.5	0.86	2
TL from CL	Juvenile-Adult	TL = 3.76 * (CL) + 0.87	266	TL=3.0-20.5	0.94	2
TL from telson	Adult	TL = 4.973 * (Telson) - 0.4994	611	TL=5.8-24.3	0.93	3
		T. spinifera				
BL from TL	Adult	BL = 0.8242 * (TL) - 0.2725	132	TL=10.4-26.5	0.99	1
BL from TL	Juvenile	BL = 0.8213 * (TL) - 0.1801	65	TL=4.5-15.3	0.99	1
BL from TL	Furcilia	BL = 0.8204 * (TL) - 0.1887	884	TL=2.4-16.5	1.00	1
BL from TL	Furcilia to Adult	BL = 0.8195 * (TL) - 0.1839	1081	TL=2.0-26.5	1.00	1
TL from BL	Adult	TL = 1.2031 * (TL) + 0.472	132	BL=8.4-21.6	0.99	1
TL from BL	Juvenile	TL = 1.209 * (BL) + 0.2792	65	BL=3.4-12.4	0.99	1
TL from BL	Furcilia	TL = 1.2129 * (BL) + 0.2504	884	BL=1.6-13.2	1.00	1
TL from BL	Furcilia to Adult	TL = 1.2192 * (BL) + 0.2301	1081	BL=1.6-21.6	1.00	1
CL from UL	Juvenile-Adult	CL = 2.56 * (UL) - 0.69	621	TL=10.2-30.4	0.85	2
TL from CL	Juvenile-Adult	TL = 2.57 * (CL) + 2.76	224	TL=10.2-30.4	0.88	2
BL from telson	Furcilia to Adult	BL= 4.1784 * (Telson) - 0.3272	187	BL=1.9-22.1	0.89	3
TL from telson	Juvenile-Adult	TL = 4.9348 * (Telson) + 0.5643	150	BL=7.3-22.1	0.85	3

		T. inermis				
TL from BL	Adult	TL = 1.1532 * (BL) + 0.9846	248	BL=7.0-21.0	0.99	4
TL from telson	Adult	TL = 6.4053 * (Telson) - 3.3993	248	BL=7.0-21.0	0.87	5
CL from UL	Juvenile-Adult	CL = 3.07 * (UL) - 1.11	239	TL=7.6-24.1	0.88	2
TL from CL	Juvenile-Adult	TL = 2.46 * (CL) + 2.99	246	TL=7.6-24.1	0.92	2
		T. raschii				
TL from BL	Adult	TL = 1.1887 * (BL) + 0.6838	530	BL=7.6-20.8	0.99	4
TL from telson	Adult	TL = 5.5247 * (Telson) - 1.1236	530	BL=7.6-20.8	0.89	5
		T. longipes				
BL from AL6	Adult	BL = 6.378 * (AL6) - 1.461	93	BL=7.1-24.0	0.99	6
TL from BL	Adult	TL = 1.2408 * (BL) + 0.3308	186	BL=7.1-19.3	0.99	4
TL from telson	Adult	TL = 4.4856 * (Telson) + 1.0208	186	BL=7.1-19.3	0.89	5

Abbreviations:	
AL6=	sixth abdominal segment
BL=	body length
CL=	carapace length
Telson=	telson length
TL=	total length
UL=	uropod length

Sources:

1. Gómez-Gutiérrez work in the Peterson lab in 2003.
2. Pinchuk & Hopcroft, 2007.
3. Peterson lab calculations.
4. Harvey et al. 2012.
5. BEST project euphausiid calculations 2008-2010.
6. Iguchi and Ikeda 2005.

Appendix 3

Questionnaire for Euphausiid Experts

Below is a questionnaire prepared by Dr. Jaime Gómez-Gutiérrez (CICIMAR, La Paz, Baja California, Mexico) and sent to euphausiid researchers world wide prior to the 2009 GLOBEC Open Science Meeting in Victoria, Canada. The questionnaire is followed by a sample response.

We are interested to know who is currently active in research that mostly involves euphausiids in their academic agenda to present a summary of krill experts in the forthcoming **Workshop 10** entitled "**Krill biology and ecology in the world's oceans"** that will be held at Victoria, Canada next June 22-26, 2009 as part of the 3rd and final GLOBEC Open Science Meeting entitled "Marine Ecosystems: from function to prediction". For this purpose we invite you to fill out this short questionnaire (**13 questions at 2 pages** that will take you about **10 minutes to fill out**). This will help us to obtain precise and updated information about your current academic status and research interest to be used exclusively for academic purposes in benefit of the advance in knowledge of euphausiid biology and ecology. A summary of this information will be shown and distributed among the scientist that attend the workshop 10 in the second discussion day in the meeting to enhance international collaboration in future research projects and integration of knowledge of euphausiid biology and ecology. **To stimulate you to fill out this form** you will receive via e-mail a complete list of krill scientist of the world and a summary of this information after the meeting, independently if you assist or not to the workshop at Victoria Canada krill meeting.

A first e-mail was sent in January to about **165 krill scientists** and unfortunately we have been receiving only **19 answered formats (12% and they were not included in this email)**. We would like to know your opinion and hopefully to obtain >75% response of the list of experts. **Please re-distribute this questionnaire to other scientists and students not included in this preliminary e-mail list of experts.**

Please send filled out query file attached to the following e-mail address: jgomezgu@gmail.com

Thank you very much for your valuable help with this questionnaire.

Sincerely,

Jaime Gómez-Gutiérrez (Mexico), jagomezg@ipn.mx (on behalf of the W10 co-chairs)
Angus Atkinson (UK), a.atkinson@bas.ac.uk
Bettina Meyer (Germany), bettina.meyer@awi.de
Bill Peterson (USA), bill.peterson@noaa.gov

Example of the questionnaire returned by Tracy Shaw

This is a questionnaire. That should be answered individually. Please distribute among your close collaborators and/or students to be filled out individually.

1) How you define yourself? **(please mark with an X only one option)**

a) I am a **krill scientist** because most of my research time is spent studying euphausiids	**x**
b) Euphausiids are only **part** of my research interest	
c) I do not work directly with euphausiids, but **I collaborate and/or publish with krill scientists**	

2) Complete last name and name and date of birth **(mm/dd/yy)**: Shaw, C. Tracy (DOB redacted)

3) Nationality: USA

4) Last degree already obtained (**mark with an X**):

Prof:	Dr:	MSc: x	Bachaelor:	Other:

5) Permanent work Institution name and address and/or current address:

Hatfield Marine Science Center

2030 SE Marine Science Drive

Newport, OR 97365

6) E-mail (preferred for academic purposes) and webpage (CV and related to euphausiids):

tracy.shaw@noaa.gov **Don't have a webpage**

7) For students. Degree in progress (**marx with an X**):

Dr:	MSc:	Bachaelor:	Other:

Institution name and address:

Title of thesis:

Possible date of defense (**mm/dd/yy**):

8) Where are the main regions where you study euphausiids (currently and in the past, mention sampling area and/or species distribution range in case of land laboratory experimental work):

Antarctica 1993-2000

Northeast Pacific (mainly OR, WA) 2001-present

Bering Sea 2008-2010

9) Which species you mostly study? (in case you study community structure mention some of the most abundant species in your study area

Antarctica: ***E. superba***

Northeast Pacific: ***E. pacifica, T. spinifera***

Bering Sea: ***T. inermis, T. raschii***

10) Which are the research topics that involve your study of euphausiids? (**mark as many topics as you consider appropriate to describe your research interest**)

Krill research topic	
a) Controls on distribution and abundance	
b) Determining absolute biomass and abundance (net/Acoustic)	**x**
c) Behaviour	
d) Reproductive biology	**x**
e) Larval biology	**x**
f) Ecophysiology and energy budget	
g) Feeding and diet	**x**
h) Population parameters: Growth rate, mortality rate	**x**
i) Parasites	
j) Developing whole/partial life cycle models	
k) Schooling and vertical migration	
l) Biogeochemical role of krill	
m) Fisheries and krill	
n) Krill in the food web (Predator-prey interaction that include euphausiids)	
o) Future impacts on euphausiids	**x**
p) Taxonomy and phylogeny	
q) Other not included in this list (mention the topic)	

11) In your opinion which is/are the main gaps in knowledge and/or **hypotheses** about euphausiids biology and ecology that should be considered in future international research programs?

1. **Diets of *Thysanoessa* spp. A better understanding of their dietary needs would allow us to maintain these animals in the lab to measure larval development and long-term growth rates and egg production as we have done for *E. pacifica*.**
2. **Basic measurements (biomass, egg production, molting, growth, feeding) conducted in different regions using the same protocols to make the results easily comparable.**
3. **Life history of *E. pacifica* in the open ocean, and the status of this species in the Bering Sea.**
4. **Understanding of how closely the timing of reproduction in different species of euphausiids is linked to seasonal cycles of phytoplankton production.**

12) Would you like to be part of a webpage list server for euphausiid experts to discuss questions, hypothesis, and/or updates to read about the latest publications about euphausiids?

Sure.

13) Would you be interested to do a further organization effort to do the Year of the Euphausiids or collaborative research in an international level? (i.e. Global collaboration on krill research using standard methods) **YES** (x) **NO** ( ).

If your answer is **YES** in which topics?

Measurements of vital rates, such as growth rates and brood sizes.

Any comment and/or idea to stimulate international collaboration to study krill around the world it is more than welcome:

The protocols used by the Peterson lab in Newport, OR, to measure euphausiid growth rates and egg production are available on the PICES website http://www.pices.int/projects/Euphasiid/euphasiid.aspx.

We are happy to answer any questions about these protocols, and encourage other researchers to conduct such studies when they have the opportunity.

Please send filled out query file attached to the following e-mail address:

jgomezgu@gmail.com

We will provide you the list of krill scientist and the summary of the results of this survey via e-mail independently if you assist or not to the krill workshop 10 at Victoria Canada.

Appendix 4

WG 23 Annual Reports and Topic Session/Workshop Summaries

PICES Seventeenth Annual Meeting, PICES-2008
October 24–November 2, 2008
Dalian, People's Republic of China

2008 REPORT OF WORKING GROUP 23 ON *COMPARATIVE ECOLOGY OF KRILL IN COASTAL AND OCEANIC WATERS AROUND THE PACIFIC RIM*

The Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* (WG 23) convened its first meeting on October 24, 2008 under the co-chairmanship of Drs. William Peterson and Song Sun. At least 16 persons attended the full workshop with perhaps the same number attending portions of the workshop. A list of those who attended the complete workshop can be found at the end of this report (*WG 23 Endnote 1*). A draft of the agenda was reviewed and adopted without changes (*WG 23 Endnote 2*).

AGENDA ITEM 2
Summary of research – Country reports

One member from each PICES member country provided a 30-minute summary of past, present and future research related to krill species in local waters, with emphasis focused on *Euphausia pacifica* and *Thysanoessa* spp. Although the presentations are not available on the PICES website, anyone interested in a certain talk can e-mail the author or Co-Chairman, bill.peterson@noaa.gov, to request a copy.

Canada
Dr. David Mackas informed the Working Group that the earliest work on life cycle, growth rate and production of *E. pacifica* in the Strait of Georgia was by Heath (1977, Ph.D. thesis). Coastwide surveys of ichthyoplankton in 1980 were used to summarize krill cohort structure and growth (Fulton *et al.* 1982). A thesis by Summers (1993) explored growth of *Thysanoessa spinifera*. Studies of long-term variations in abundance of *E. pacifica* and *T. spinifera* have been carried out by Tanasichuk (1998); Dr. Mackas tracks long-term changes in abundance from his sampling program off the west coast of Vancouver Island, including the study of cross-shelf transport and retention mechanisms, and patchiness and their causes have been investigated recently. Dr. Steve Romaine (DFO, Institute of Ocean Sciences) has developed algorithms for calculating the patch structure of krill from acoustic surveys in the Strait of Georgia. Strengths of the Canadian program are: spatial distribution, population dynamics, and a long time series. Gaps include the need for work on live animals, especially for rates of metabolism and reproduction, and the study of mechanism(s) of population regulation, including reproduction, predation and parasites.

China
Dr. Song Sun stated that the dominant species in Chinese waters are *Euphausia pacifica* and *Pseudeuphausia sinica.* Most of the work in China is focused on sampling and experimental work in the Yellow Sea and the East China Sea, but with some research on the Antarctic krill *Euphausia superba. Euphausia pacifica*, along with the copepod *Calanus sinicus*, are the dominant species in both the Yellow and East China seas, and thus receive most of the research attention. Major research cruises were carried out monthly in summer and quarterly in winter to determine krill distribution and abundance. They are most abundant in the middle of the relatively shallow Yellow Sea (maximum water depths of about 90 m) with a maximum in adult biomass in the autumn. Maxima in abundances of eggs are in the spring, similar to that reported for the northeast coast of Japan. Egg production experiments showed that spawning is most intense in March–May, averaging about 40 eggs per female in April and May. A major piece of research needed is to understand how the adults survive the very warm summer months when surface waters in the Yellow Sea can exceed 25°C. Apparently the adults reside in the deeper (and colder) waters of the Yellow Sea and migrate each night to the base of the pycnocline to feed on phytoplankton.

Japan

Dr. Yuji Okazaki presented an "*Overview of krill biology and ecology in the western North Pacific*". He reported on the krill fishery off the east coast of northern Japan – the fishery takes place from February to May and is well-regulated. Krill are harvested mostly for the aquaculture industry but some are dried for human consumption. In terms of research, the published work of Taki on distribution (including vertical distribution), abundance and growth was reviewed. Some new work on egg production was presented showing that *Euphausia pacifica* can lay eggs during temperatures as low as 5°C in April, at the time of the spring bloom; the major spawning season is April–May; egg production measurements have been made April–July, with an average output of approximately 60 eggs per female. Dr. Okazaki also reviewed Japanese work on *Thysanoessa* spp. and noted that they seldom make up more than 10% of the total euphausiid biomass. New work is now being prepared for publication on *Thysanoessa* by Taki and Kim from Hokkaido University. The available historical data were reviewed, and Dr. Okazaki noted that the euphausiids from the Odate collection have not been analyzed but cautioned that the small mouth of the Norpac net may have resulted in low catches of krill. Collections from the PH-line (off Hokkaido) are being processed for eggs and larvae, and taxa that likely do not avoid plankton nets. Future work is planned to concentrate on sampling along the A-line which will focus on comparison of krill in nets of various sizes (bongo *vs*. MOHI net), and on growth rate experiments.

Korea

The Korean report was given by Dr. Hyoung-Chul Shin. Surveys of krill in Korean waters have been conducted by the National Fisheries Research and Development Institute (NFRDI) on a bimonthly basis but these samples have not been processed for krill eggs, larvae, juveniles or adults. Surveys of krill in the Yellow Sea in spring and fall were reported by Yoon (2000). Distributions seemed to be controlled more by temperature than by chlorophyll. Dr. Shin also reported on some work carried out at a nuclear power plant – the screens for water intake used for the cooling towers can at times be clogged with *Euphausia pacifica* – we heard a report on this at the krill Topic Session on "*Life history and ecology of euphausiids in coastal and oceanic waters around the Pacific Rim*" (S2) (Chae, PICES XIV). The potential is great for additional work on krill in Korean waters and plans are being discussed that may lead to new work on distribution, abundance, feeding, egg production, and growth. Ships are available for surveys and in-house expertise exists for identification of krill as well as the use of acoustics during krill surveys that could be used to estimate krill biomass and patch structure. There is also expertise on lipid analysis that would help clarify krill's role in the food chain.

Russia

Dr. Yury Zuenko stated that there are no scientific programs focused on euphausiids in Russia. However, euphausiids are (and were always) studied as a part of the zooplankton community. General information is available on zooplankton resources, distribution, species composition, and biology of the main species, including euphausiids, in the Far-Eastern Seas and Northwest Pacific. Within regional ecosystem-based programs, the Pacific Research Institute of Fisheries and Oceanography (TINRO-Centre) conducts annual surveys of zooplankton (sometimes twice in a year) over the Okhotsk Sea and western Bering Sea, and off the Kuril Islands. From time to time (once in 3–4 years) the northern Japan Sea is surveyed. Foreign EEZs are surveyed within bi-lateral programs with Japan and the U.S.A. (previously also with the Democratic People's Republic of Korea (North Korea) and China). Again, although krill are not the target species, they are collected in the plankton nets but probably only the eggs and larvae are collected quantitatively. Although many samples have been collected, many need to be analyzed, giving the opportunity for joint collaborative work. There are as yet no plans for any experimental work although such work could move forward with proper training.

U.S.A.

Ms. Tracy Shaw reviewed the research that has been carried out in the California Current, Gulf of Alaska and Bering Sea by as many as 30 investigators. Her comprehensive talk covered work in the laboratory on vital rates, including developmental times, bioenergetics, physiology and respiration, feeding, growth and reproduction. Field work on age structure, seasonal cycles of spawning, seasonal and interannual variations in brood sizes, and growth were compared. She also reviewed synthesis activities planned by the U.S. GLOBEC program.

AGENDA ITEM 3
Gaps in krill research that need to be filled

WG 23 prepared an outline which listed the gaps in knowledge and plans for research that will fill those gaps. The Working Group discussed what research needed to be done to produce a synthesis and comparison of the ecology, life history and population dynamics of krill around the Pacific Rim.

1. Standardization of sampling through use of the same nets, or, if this is not possible, the need for "catchability coefficients" of krill by various types of nets. Better estimates of abundance and biomass are needed in order to be able to make regional comparisons.
2. Size of animals in different regions and seasonal differences in size; comparative length-weight regressions.
3. Feeding habits and diets through experimental work on living animals and through use of lipid biomarkers and stable isotopes.
4. Aggregations of krill. This needs more study – what are the advantages to an individual for staying within a swarm? Are there physiological benefits? More night sampling is needed.
5. Age of adults. More work is needed to explore the utility of the lipo-fuscein method of age-determination.
6. Sampling in critical habitats. Are there "critical habitats" that we are not sampling and which need more study? Suggested examples include the Japan/East Sea, particularly in Korean waters, Monterey Bay (CA), Heceta Bank (OR), Unimak Pass (AK), Northeast Japan.
7. Use of acoustics to estimate biomass and patch structure.
8. Modeling of krill.
9. More measurements of egg production rates in relation to temperature and chlorophyll.
10. A project that looks at population structure using modern techniques of microsatellites or SNPS is needed to determine the degree to which populations of *Euphausia pacifica* are connected.
11. An interest was expressed in setting up a "krill library" where all important publications could be available. This would include theses, cruise reports, and grey literature. Ideally, all would be available in English.
12. All participants expressed interest in having a set of digital photographs of krill life cycle states that could be used in presentations. Also, any video clips showing krill aggregations would be of interest as well. These could all be stored on the same website where the "krill library" was maintained. The need to find a "home" for this material, perhaps on the PICES webpage was discussed.

Also discussed was the possibility of using krill in NEMURO models that would compare zooplankton population dynamics in waters around the Pacific Rim (see for example a recent paper by Terui and Kishi (2008), Population dynamics model of Copepoda (*Neocalanus cristatus*) in the northwestern subarctic Pacific. Ecological Modelling 215: 77–88.)

A final report was given by Dr. Micho Kishi, Hokkaido University, Japan. He reviewed progress on his and his student's work on incorporating krill into the NEMURO modeling framework. The model has stage-specific feeding rates, with larvae feeding on two size-classes of phytoplankton, and juveniles and adults feeding on both phytoplankton and on copepods. Developmental rates and transition times between stages follow data in Ross (1982). The model seemed to do a reasonable job in tracking the seasonal cycles of abundance of eggs, larvae, juveniles and adults, given the agreement between the model and observations of Taki (2004), and reported by Dr. Okazaki in Japan's report (Agenda Item 2).

AGENDA ITEM 4
Exchange of scientists, graduate students and post-docs

The Working Group discussed the potential for an exchange of scientists, graduate students, and post-docs in order to learn from one another how best to sample euphausiids and how to conduct experimental work on living krill. Also discussed were any cruise plans for 2008–2009 that would benefit from international

cooperation; possible visits to other laboratories; and the possibility of convening "hands-on" practical workshops during which the Working Group would teach students and other scientists how to carry out experimental work with krill

AGENDA ITEM 5
General discussion

A portion of the general discussion was set aside to hear a talk by Dr. Jaime Jahncke on "*Krill related studies in the Gulf of the Farallones, California*". This contribution was to be a poster presented during the Poster Session of main PICES Annual Meeting but seemed that it would be useful to include it during our meeting. The talk included discussion of a large research program that is working on spatial and temporal relationships between krill and seabirds that nest on island in the Gulf of the Farallones, located offshore of San Francisco. Of particular interest is krill patchiness and patch size and how this relates to forage opportunities for the sea birds, in particular the Cassin's auklet.

Most of the remaining time was devoted to a general discussion of the krill workshop planned for the GLOBEC Open Science Meeting to be held in Victoria June 2009. The workshop, entitled "*Krill biology and ecology in the World's oceans*", is being organized by Dr. Peterson along with Drs. Angus Atkinson, Bettina Meyer and Jaime Gómez-Gutiérrez (*WG 23 Endnote 3*). The objective is to convene a gathering of krill biologists and ecologists from around the world to discuss the life history and population dynamics of all krill species. These discussions were first initiated at the 4th International Zooplankton Production Symposium in Hiroshima, Japan, May 2007. A number of Working Group members agreed to submit abstracts for the GLOBEC meeting – Yuji Okazaki, Song Sun, Hyoung-chul Shin, David Mackas and William Peterson.

WG 23 Endnote 1

WG 23 participation list

Members	Observers
Se-Jong Ju (Korea)	Harold Batchelder (U.S.A.)
Hyung-ku Kang (Korea)	Hongsheng Bi (U.S.A.)
David Mackas (Canada)	Jaime Jahncke (U.S.A.)
Yuji Okazaki (Japan)	Michio J. Kishi (Japan)
William T. Peterson (Co-Chairman, U.S.A.)	Bernard Megrey (U.S.A.)
C. Tracy Shaw (U.S.A.)	Jennifer Menkel (U.S.A.)
Hyoung Chul Shin (Korea)	Tom Wainwright (U.S.A.)
Song Sun (Co-Chairman, China)	Yury Zuenko (Russia)

WG 23 Endnote 2

WG 23 meeting agenda

1. Welcome and introductions
2. Summary of past, present and future research related to krill species in local waters
3. Discuss the gaps and plans for research that will fill those gaps.
4. Discuss the potential for an exchange of scientists, graduate students, and post-docs.
5. General discussion

WG 23 Endnote 3

Proposal for a 2-day workshop at the GLOBEC Open Science Meeting in June 2009 in Victoria, Canada, on "*Krill biology and ecology in the World's oceans*"

Chairs: Angus Atkinson (UK), Jaime Gómez-Gutiérrez (Mexico), Bettina Meyer (Germany) and William Peterson (U.S.A.)

Objective: To convene a gathering of krill biologists and ecologists from around the world to discuss the life history and population dynamics of all krill species. This is timely because krill have been important elements of a number of the GLOBEC core programs and a great deal has been learned from the GLOBEC fieldwork that needs to be synthesised. These discussions were first initiated at the 4th International Zooplankton Production Symposium, in Hiroshima, May 2007. At that meeting we convened a workshop and were overwhelmed with presentations (42 oral and poster presentations) and attendance (approx 100 participants). A product of the meeting was a special issue of selected papers from the Symposium to be published in *Deep-Sea Research II*; the special issue is now in the final editing phase. A total of 18 research papers have been found to be acceptable for publication.

Aims of the proposed GLOBEC OSM Workshop include:

- For workers on different species to get together to discuss methods/approaches that have proved effective for one species. Then we can see whether they can be applied to other euphausiid species.
- To make sure there is a degree of harmony (or at least that there is no serious disconnect) in their approaches. It is also to improve technical aspects of specific methods.
- To generate ideas for future collaborations, for example laboratory/seagoing exchanges of personnel and of exchange and pooling of datasets to address wider-scale issues.
- To produce a tangible product, to show where krill research is at the moment, hurdles to progress and potential solutions. We suggest that an overview type paper in MEPS/review length journal (authored *e.g.*, by all participants) would be excellent.

We propose a 2-day workshop, with the first day being a series of short 10-minute presentations with, say, a 5-minute discussion around each (15 minutes total). These presentations would have some data (obviously) as examples, but would aim to give more of a flavour of the state of the research in their own lab/research group in relation to the session theme, with some questions, future directions and "hooks" to start the discussion. The second day could then be devoted to framing particular themes and issues for more detailed discussion, then breakout groups, *etc.*, before coming together at the end to talk about how we are all going to put together the written product. We expect active participation by young investigators and graduate students.

The Table below shows some topics that may be valid, with some potential speakers/contributors. This is clearly incomplete and of course there is some overlap across themes. Also note that some topics, *e.g.*, modelling and genetics, are blended across several themes. An alternative approach would be to have them as separate, defined themes.

Topic	Possible speakers	Notes
Controls on Distribution	Peterson, Zhou, Goodall-Copestake, Atkinson	- To what extent are euphausiids drifters in ocean currents? - Use of advective models to understand distribution, - Role of swimming/vertical migration in dictating distribution, - Combining historical datasets for a larger-scale understanding of distribution, - Contrasting controls in upwelling areas, S Ocean, N Atlantic and N Pacific Genetic approaches to stock separation – functional and genetically defined sub-pops.
Determining absolute biomass and abundance	Demer, Watkins/Fielding, Nicol	- How reliable are nets and acoustics in determining absolute abundance/biomass? - Can we make better efforts to combine them?

Topic	Possible speakers	Notes
Behaviour	Kaartvedt, Yen, Kawaguchi, Brierley	- Role of laboratory/experimental studies, - Sensory biology, - Role of underwater cameras/ROVS, *etc*. - Role of moored instrumentation and advanced acoustics (*e.g.*, to determine swimming/migration speed in *M. norvegica*, *etc.*).
Reproductive biology	Gómez-Gutiérrez, Cuzin	- What affects reproductive output? - Food quantity/quality effects and egg condition/viability, - Spawning periodicity – field and histological approaches.
Larval biology	Meyer Shaw/Feinberg	- Critical phases concept, - Alternative developmental pathways (*e.g.*, intermediate/missed stages), - What can we learn from inter-species comparisons?
Ecophysiology and Energy budget	Ross/Quetin, Daly, Taeshke, Tarling, Jarman, Teschke	- What dictates moulting frequency? - Is moulting a "pacemaker" for maturation/spawning? - Issues with measuring rate processes in euphausiids, - Cues for seasonal behaviour (hormones *vs.* external cues) experimental and genetic approaches, - What are main unknowns in the energy budget - does not knowing them matter? - Role of lipids across different krill species – are their common themes?
Feeding and diet	Passmore, Schmidt, Stuebing, Kaartvedt	- Evaluation of emerging methods (*e.g.*, immunoassays, quantitative genetics), - Value of combined methods, - Application from one species (*e.g.*, paired mandible method for *M. norvegica*) to others, - Evaluating specific issues with gut contents, feeding incs, FA biomarkers, stable isotopes.
Population parameters: Growth rate Mortality rate	Pinchuk, Feinberg/Shaw, Gómez-Gutérriez, Mortality rate expert needed	- "Standardising" IGR approaches, - Methods to evaluate length frequency data, - Comparison of growth rates across euphausiid species, - Methods of determining mortality rate, - Sources of mortality: predation versus parasitism/pathogens/"old age".
Developing whole/partial life cycle models	Hofmann, Tarling, Fach, Murphy	- Where are we at with the various species? - Identifying key knowledge gaps and how to address them.
Schooling and vertical migration	Zhou, Kaartvedt, Tarling, Mangel/Alonzo, Hofmann, Sourisseau/Simard	- Inter-species comparison of extent of schooling/vertical migration, - Behaviour and characteristics of schools, - Advantages and disadvantages of schooling (including modelling approaches), - Variability in DVM and costs/benefits (including modelling approaches), - DVM and schooling as mechanisms for retention/efficient swimming.
Future impacts on euphausiids	Kawaguchi, Ross	- Changes in temperature/ice cover/food/ phenology/ph – approaches to predicting the future, - Timescale of change and rates of adaptation to change, - Other challenges: pollution, UV, harmful algal blooms, *etc*.

PICES Eighteenth Annual Meeting, PICES-2009
October 23–November 1, 2009
Jeju, Republic of Korea

REPORT OF WORKING GROUP 23 ON *COMPARATIVE ECOLOGY OF KRILL IN COASTAL AND OCEANIC WATERS AROUND THE PACIFIC RIM**

The meeting of Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* (WG 23) held its second meeting on October 23, 2009 in Jeju, Korea. A list of participants and the meeting agenda can be found in *WG 23 Endnotes 1* and *2*. The meeting was chaired by Ms. Tracy Shaw, as the Co-chairs, Drs. Song Sun and William Peterson, were unable to attend.

AGENDA ITEM 2
Presentation on status of krill research in each PICES member country

The meeting started with presentations on the status of krill research in each PICES member country that had a representative in attendance: Canada (Mackas), Japan (Okazaki), Korea (Ju), U.S.A. (Shaw). These presentations were based on the Working Group's Term of Reference #6 (Convene a krill workshop at the GLOBEC Open Science Meeting in May 2009). This led to discussion of what topic to address in the first synthesis paper and what data to collect to enhance the available data set. Brood sizes of *Euphausia pacifica* were a likely candidate as scientists in China and Japan have recently conducted such experiments and there is a possibility that scientists from Canada and Korea will be able to conduct brood size experiments during their research cruises next year. Collection of such data is ongoing in Dr. Peterson's lab at the Northwest Fisheries Science Center (NOAA) and there is a hope to recruit other scientists working on the California Current.

AGENDA ITEM 3
Specific terms of reference (TOR)

The other main topic of discussion (TOR #1) was on assembling lists of existing data that will contribute to an analysis and comparison of the life histories of *E. pacifica* and *Thysanoessa*. Egg production, development times, growth rates, distribution and abundance, migration, biomass, hot spots, seasonality of spawning in relation to phytoplankton blooms, role of krill as grazers, vertical flux of carbon in fecal pellets (and moults?) had been discussed previously and to this list krill strandings were added. The latter are reported regularly and, although there are many theories as to why they occur, they are not well understood.

The translation into English of papers which would facilitate a comparative ecological analysis is another goal of this Working Group. Noting that translation of entire papers is a tremendous project, the Group considered translating only parts of each paper (such as the abstract and conclusions) and expanding the figure captions to include more detail. It is possible that this could be done cooperatively by members of the Working Group. Upon completion, the documents could be made available via the PICES website.

AGENDA ITEM 4
Research during PICES/ICES/FAO symposium

WG 23 members discussed the possibility of "hands-on" research in association with the PICES/ICES/FAO Symposium on "*Climate change Effects on Fish and Fisheries*" in Sendai, Japan, from April 26–29, 2009. Dr. Yuji Okazaki will look into the possibility of a visit to his lab at the Tohoku National Fisheries Research

Institute in Shiogama, Japan. The Peterson lab at Oregon State University, U.S.A. has been invited to participate on a Korean research cruise in 2010. These two activities are in accordance with TORs #2 (Prepare a research plan to help fill gaps in our understanding, and aid regional collaborative research efforts. Explore ways and means of facilitating exchange of scientists between laboratories and on research cruises) and #3 (Convene "hands-on" practical workshops with krill biologists (including students and established scientists) from PICES member countries to help them initiate and carry out krill research programs. These workshops could be convened before each PICES Annual Meeting, or at other times as appropriate. Protocols for experimental work have been already published on the PICES website at http://www.pices.int/projects/Euphasiid/PICES%20Protocols%20COMPLETE.pdf).

AGENDA ITEM 5

Attendance at Workshop W4 on "*Marine ecosystem model inter-comparisons*" at PICES-2009

WG 23 discussed collaboration with PICES modelers (TOR #5; Work with modelers to better parameterize euphausiids in the NEMURO model and other models so as to explore their role in coastal and oceanic food chains). Specifically, that euphausiid modeling should incorporate the differing characteristics of different life stages, *i.e.*, in a model, early larval stages behave similarly to a copepod but older life stages behave quite differently from copepods. Dr. David Mackas reported on the modeling efforts of Dr. David Preikshot at the University of British Columbia, Canada. He is using ECOPATH to model different life stages of euphausiids and is including gelatinous zooplankton, with approximately monthly time steps.

WG 23 Endnote 1

WG 23 participation list

Members	Observers
Michael J. Dagg (U.S.A.)	Harold Batchelder (U.S.A.)
Se-jong Ju (Korea)	Hye-Seon Kim (Korea)
Hyung-ku Kang (Korea)	
Michio J. Kishi (Japan)	
David L. Mackas (Canada)	
Yuji Okazaki (Japan)	
C. Tracy Shaw (U.S.A.)	

WG 23 Endnote 2

WG 23 meeting agenda

1. Welcome and introductions
2. Presentation on status of krill research in each PICES member country
3. Discuss specific terms of reference
4. "Hands-on" research during PICES/ICES/FAO symposium on "Climate change effects on fish and fisheries"
5. Attendance at WS 4 on "*Marine ecosystem model inter-comparisons*" at PICES-2009

*Post-Jeju Progress

Based on discussions at the WG 23 meeting at Jeju, the following actions have taken place:

1. A synthesis manuscript is being prepared by Leah Feinberg on pan-Pacific variations in brood sizes of *Euphausia pacifica* based on recent experiments conducted in the southern California Current. We will present results of that effort at the Portland meeting.

2. Requests were made for each WG member to bring to the Portland meeting metadata that describes data and publications such that we can discuss types of other synthesis papers we might be able to begin to write within the next year.

3. Yuju Okazaki arranged a tour of the Tohoku National Fisheries Research Institute laboratory following the Sendai meeting (April 2010).

4. Hal Batchelder arranged a meeting with an Oregon State University librarian and the Peterson lab to discuss with her the legal issues with posting pdf files of scientific papers to a WG 23 Website. She suggested we use **Zotero** [zoh-TAIR-oh] which is a free, easy-to-use Firefox extension to help one collect, manage, cite, and share research sources. According to their web-page, it lives right where you do your work—in the web browser itself. This seems like a good way to share data and publications. We will discuss this in Portland. Apparently Zotero is able to link citation information which has been entered to online electronic archives provided by the publishers, and may serve as the best way for providing access to publications.

5. A research cruise with Korean scientists to the Yellow Sea, arranged by Se-Jung Ju for April 2010, had to be postponed to a later date as a result of the sinking of the Korean Navy ship. Bill Peterson and Tracy Shaw were to participate in this cruise.

6. Bill Peterson was allocated some start-up funds to begin study of pan-Pacific variations in genetic structure of our study organisms, *Euphausia pacifica*. A recent doctoral student, Mattias Johansson has been hired to begin this work.

7. Se-Jung Ju has collected *Euphausia pacifica* from Korean waters (both east and west sides of Korea) and has preserved them in alcohol for later analysis of genetic structure. Tracy has done the same with *E. pacifica* collected from the Bering Sea so we now have specimens from three widely-separated locations.

8. Peterson lab hosted a Chilean graduate student, Ramiro Riquelme, this summer. We learned from him how to do measurements of the hepatopancreas length as a measure of euphausiid condition. We will report on this technique at the WG 23 meeting in Portland with the hope that other members of WG 23 will adopt this method in their future research.

9. The Peterson lab continues to host a Chinese graduate student, Xiuning Du (from Ocean University of China, in Qingdao), who is working on feeding rates and food preferences of *Euphausia pacifica* through microscopic counts of phytoplankton and ciliates removed in control vs feeding containers. She will be giving an oral presentation on her work at the Portland PICES meeting (BIO Session).

10. The Krill Special Issue appeared in April 2010 and those who have seen it have commented that it is really nice and well worth the wait.

PICES Nineteenth Annual Meeting, PICES-2010
October 22–31, 2010
Portland, U.S.A.

REPORT OF WORKING GROUP 23 ON *COMPARATIVE ECOLOGY OF KRILL IN COASTAL AND OCEANIC WATERS AROUND THE PACIFIC RIM*

The Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* (WG 23) held its third meeting on October 24, 2010, from 0900–1230 h under the chairmanship of Dr. William Peterson who welcomed the members of the Working Group who were present as well as visitors (*WG 23 Endnote 1*), and shared apologies for those unable to attend.

AGENDA ITEM 2
Agenda additions and/or changes

The Chairman asked if there were any additional change to the agenda. The only item offered was the need to discuss where we could to dinner that evening. The meeting agenda can be found in *WG Endnote 2*.

AGENDA ITEM 3
Country reports

Reports from each PICES member country on progress during the past year were given. These reports were to include a variety of items including (1) status of metadata describing data which exists (which data can be easily shared for synthesis papers); (2) publications to be included in our publications data base; (3) status of the idea of having portions of papers written in other languages translated into English; (4) potential for collaborative research in the near future; (5) TOR # 5 – status of Working Group members' work with modelers.

Canada

Dr. David Mackas summarized the extent of krill sampling in Canada, carried out by four programs. First, the ocean sampling that his group has been doing for a number of years was summarized. This, the "IOS Time Series" continues with 3–6 surveys per year, with sampling off southern Vancouver Island, northern Vancouver Island and Hecate Strait. Cruises are most often in May/June, August/September, depending on the availability of ship time. Sampling includes bongo tows during both day and night from which biomass per square meter is calculated. Another important time series is the one conducted by Dr. Ron Tanasichuk (Pacific Biological Station). He samples in Barkley Sound, with 10 surveys per year since 1991. Samples are processed chiefly for krill which are catalogued by length, weight, sex, maturity, gonad weights, and larval stage. Third, surveys also take place in the Strait of Georgia. These have been intermittent since 1968; the nighttime samples have been analyzed for euphausiids. Ms. Moira Galbraith (Institute of Ocean Sciences) maintains the database. Grad student Lingbo Li (University of British Columbia) has been analyzing the data from these samples and reports that there appears to be a big drop in the biomass of *Euphausia pacifica* in Strait of Georgia and an increase in *Thysanoessa spinifera* over the past 10 years. Finally, the cabled observatories, the NorthEast Pacific Time-Series Undersea Networked Experiments (NEPTUNE) and the Victoria Experimental Network Under the Sea (VENUS) projects include a 125 kHz echosounder (single frequency), and "krill" signals are being analyzed by Mei Sato (University of Victoria graduate student) with Dr. John Dower (University of Victoria).

China

No report was available.

Japan

Dr. Yuki Okazaki reported on several activities. First, information on the vertical distribution of early life stages of *E. pacifica* was presented at the PICES/ICES/FAO Symposium on "*Effects of climate change on fish and fisheries*" held in Sendai, Japan, in April 2010. Second, they have begun to do some feeding experiments on adult krill during their cruises, with the first experiments carried out in June 2010 in the Oyashio. In a related effort, they will use the Odate/NORPAC net collections to look at eggs and larvae of *Euphausia pacifica*. Pilot studies are underway. They have also been looking at samples from the A-Line (2001–2008), PH Line (1980–2000) and the Saury surveys (2001–2007). They have found that euphausiid larvae were mostly found at stations with a depth of ~100 m and temperature < 12°C. Larvae were most abundant May/June coincident with phytoplankton blooms at that time of the year. Calyptopis and furcilia densities are similar in shelf and offshore waters. For much of this work, collaborations have been initiated with Dr. Tomohiko Kikuchi (Yokahama National University) and his PhD student. It is possible that collaboration will soon be established with Dr. Yoshinari Endo (Tohoku University) on krill and climate change. Finally, Dr. Okazaki expressed interest in working with the Peterson lab on population genetics of *Euphausia pacifica*.

Korea

Dr. Se-Jung Ju reported that there are many samples available from Korean waters that can be analyzed for krill eggs, larvae, juveniles and adults, including bi-monthly samples collected by the NFRDI, since 1968. However, he noted that many samples do not look good due to drying out. KORDI samples the East Sea and East China Sea in spring and summer and there are opportunities for others to join these cruises to sample euphausiids and to conduct experiments on living animals. He noted that Korean scientists tried some live animal experiments but without much success. They incubated 35 females but only 2 spawned 103 and 136 eggs per female, respectively. He is also doing lipid analysis on some krill collected from recent cruises.

Dr. Ju also presented an overview of studies of krill life cycles in the Yellow Sea Cold bottom water. By studying the acoustically-derived scatter layer, it was determined that the migration speeds of the krill scattering layers were 0.87 m day (downward at dawn) and 0.74 m day (upwards at night) in spring. Rates were different during summer: 0.44 m day (down) and 0.49 m day (up) in summer. In summer they only migrated to the base of the mixed layer where the water is still cold and where the Chl maximum is found.

Future work will include studies of the feeding ecology of krill using trophic lipid markers. Acoustics data from daytime suggests that adults are living on the bottom during the day. Thus it might be interesting to attempt to sample the adults with bottom sampling nets. Future work will also include two cruises per year, spring and summer, and these will involve net tows, acoustics for DVM, and additional lipid work.

To date, Korean scientists have published about 8 papers, 3 of which are in Korean.

Russia

No report was available.

U.S.A.

Sampling along the Newport Line is continuing every two weeks; the Peterson lab initiated feeding experiments on *Euphausia pacifica* and work was being carried out by a Chinese Ph.D. student, Xiuning Du. Dr. Peterson also summarized many of the items discussed in the following agenda items.

AGENDA ITEM 4
Progress report on *Euphausia pacifica* synthesis paper

Ms. Leah Feinberg (Oregon State University) presented a report on the synthesis of *Euphausia pacifica* brood sizes. This paper will be similar to one published in 2006 by Dr. Jaime Gómez-Gutiérrez (CICIMAR) and others on *Euphausia pacifica* where brood size as a function of body length were compared using data from Puget Sound (Ross), the Sea of Japan (Iguchi) and Oregon (Peterson lab). She has updated that paper using data from the Oregon coast 2003–2007 (n = 368), the Gulf of Alaska (n = 60), the Southern California CalCOFI region (Decima, n = 84), and the Oyashio (Okazaki, n = 59). She has some data from the Yellow Sea (from Se-Jung Ju) but is still waiting for some data from Dr. Song Sun (China). She also needs to standardize the lengths (some people use total length, others body length). She is finding the same dome-shaped relationship as before, but with many more data points.

AGENDA ITEM 5
Using Zotero as a way of sharing published papers

WG 23 discussed the use of this tool as a way to store pdf files of published papers and other documents on the PICES website. Dr. Harold Batchelder arranged a meeting with an Oregon State University librarian and the Peterson lab to discuss with her the legal issues of posting pdf files of scientific papers to a WG 23 website. She suggested using Zotero which is a free, easy-to-use Firefox extension to help users to collect, manage, cite, and share research sources. According to the Zotero webpage (www.zotero.org), it lives right where you do your work—in the web browser itself. Zotero is able to link citation information which has been entered to online electronic archives provided by the publishers, and may serve as the best way for providing access to publications. WG 23 agreed that the tool seems like a good way to share data and publications.

AGENDA ITEM 6
Status of new project to characterize genetic structure of *Euphausia pacifica*

At the time of the meeting, it was reported that Dr. Peterson had hired a post-doc at the Hatfield Marine Science Center (Dr. Mattias Johansson) to begin some exploratory work on the population genetics of krill. Considerable progress has been made and will be reported on at PICES-2011 in Khabarovsk, Russia.

AGENDA ITEM 7
Report on the potential for using measurements of hepato-pancreas size as an index of condition in *Euphausia pacifica*

As with the genetics work, it was reported that we had only the potential to add measurements of the hepato-pancreas to our tool box. The Peterson lab hosted a young Chilean scientist, Ramiro Riquelme, during August 2010 in Newport, to collect living krill during our biweekly cruises and to measure the size of the hepato-pancreas. We learned that this appears to be a promising index of recent krill growth.

AGENDA ITEM 8
Discussion of TOR # 7

WG 23 discussed whether or not there was enough new information to justify organizing a krill symposium or a krill Topic Session for PICES-2011 in Khabarovsk, Russia. It was decided to not pursue this.

AGENDA ITEM 9
Summary of mid-term activities

A summary of activities of WG 23 following PICES-2009 in Jeju, Korea, and preceding PICES-2010 is reported in the following:

1. A joint Korea–U.S. research cruise was scheduled for April 11–18, 2010 with the purpose of training Korean scientists on how do carry out ship-board laboratory studies of krill egg production, molting and grazing. Unfortunately the cruise was cancelled (on April 7) because the research ship was requested to help investigate the causes of the sinking of a Korean Navy ship at the end of March. Ms. Tracy Shaw and Dr. Peterson were to have joined this cruise, led by Dr. Se-Jong Ju, all of whom are Working Group members.

2. Dr. Peterson was allocated some start-up funds to begin study of pan-Pacific variations in genetic structure of our study organisms, *Euphausia pacifica*. A recent doctoral student, Mattias Johansson, was hired to begin this work.

3. Dr. Ju has collected *Euphausia pacifica* from Korean waters (both east and west sides of Korea) and has preserved them in alcohol for later analysis of genetic structure. Ms. Shaw has done the same with *E. pacifica* collected from the Bering Sea, so we now have specimens from three widely-separated locations.

4. The Peterson lab hosted a Chilean graduate student, Ramiro Riquelme, this summer. We learned from him how to do measurements of hepato-pancreas length as a measure of the euphausiid condition. [This technique was reported on at the WG 23 meeting during PICES-2010 (see Agenda Item 7) with the hope that other members of the Group will adopt this method in their future research.]

5. The Peterson lab continues to host Chinese graduate student, Xiuning Du (from Ocean University of China, in Qingdao), who is working on feeding rates of *Euphausia pacifica* through microscopic counts of phytoplankton and ciliates removed in control *vs.* feeding containers. [She was awarded Best Oral Presentation for her talk on "Feeding rates of adult *Euphausia pacifica* on natural particle assemblages in the coastal upwelling zone off Oregon, USA" for a BIO-sponsored Session at PICES-2010.]

6. A special issue of selected papers on krill from the 4th International Zooplankton Production Symposium on "*Human and climate forcing of zooplankton populations*" first appeared online in *Deep-Sea Research II*, and those who have seen it have commented that it is really nice and well worth the wait. The hard-copy of the journal was published in April 2010 (*Deep-Sea Research II*, Vol. 57, Is. 7–8). Due to the untimely death of Dr. Ed Brinton, we decided to dedicate the Krill Special Issue in his honor. Elsevier Press agreed that it was appropriate so Dr. Mark Ohman (Scripps, U.S.A.) and Jaime Farber Lorda (CICESE, Mexico) wrote up a brief obituary.

7. Tracy Shaw *et al.*'s paper on "Growth of *Euphausia pacifica* in the upwelling zone off the Oregon coast", pp. 584–591, was published in the krill special issue of *Deep-Sea Research II* in which she summarized and synthesized all published growth rate data on *Euphausia pacifica*.

8. Drs. Peterson and Kazuaki Tadokoro organized a copepod and krill workshop titled, "*Examining the linkages between physics and fish: how to zooplankton and krill data sets improve our understanding of the impacts of climate change on fisheries?*" on April 25, 2010 at the PICES/ICES/FAO Symposium on "*Effects of climate change on fish and fisheries*" held in Sendai, Japan.

9. Dr. Yuju Okazaki arranged a tour of the Tohoku National Fisheries Research Institute laboratory following the Sendai symposium (April 2010) and, despite the rainy weather on Saturday following the symposium, the tour did take place.

WG 23 Endnote 1

WG 23 participation list

Members	Oberservers
Michael J. Dagg (U.S.A.)	Xiuning Du (China)
Se-Jong Ju (Korea)	Leah Feinberg (U.S.A.)
Michio J. Kishi (Japan)	
David L. Mackas (Canada)	
Yuji Okazaki (Japan)	
William T. Peterson (U.S.A., Chairman)	

WG 23 Endnote 2

WG 23 meeting agenda

1. Welcome and introduction
2. Agenda additions and/or changes
3. Country reports on progress during the past year on action items identified at PICES-2009
   - 3.1 metadata describing data which exists (which data can be easily shared for synthesis papers);
   - 3.2 publications to be included in our publications data base
   - 3.3 status of the idea of having portions of papers written in other languages translated into English
   - 3.4 potential for collaborative research in the near future
   - 3.5 TOR # 5 – status of your work with modelers
4. Report on progress on synthesis paper on *Euphausia pacifica* brood sizes
5. Discussion (and possible demonstration) of use of Zotero as a way of sharing published papers
6. Report on status of new project to characterize genetic structure of *Euphausia pacifica* from specimens collected off Oregon, Bering Sea and waters adjacent to the Korean peninsula
7. Report on the potential for using measurements of size of the hepato-pancreas as an index of condition in *Euphausia pacifica*.
8. Discussion of TOR # 7
9. Summary of mid-term activities

PICES Twentieth Annual Meeting, PICES-2011
October 14–23, 2011
Khabarovsk, Russia

Report of Working Group 23 on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim*

The annual meeting of the Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* (WG 23) was convened in Khabarovsk, Russia, at 0900 h on October 16, 2011. Only 6 of 17 members were able to attend, and 4 observers participated (*WG Endnote 1*). Most of those who could not attend sent their regards to the U.S. Co-Chairman, Dr. William Peterson. The meeting agenda can be found in *WG 23 Endnote 2*.

AGENDA ITEM 2
Status of posting references and papers

The meeting began with a discussion of the status of posting of references and pdf copies of published papers to our ZOTERO web-page. ZOTERO is a web-based bibliographic site where documents can be stored and shared openly with WG members. The idea is that representatives of the member countries will post publications, reports and theses to this website focusing on works available in their own country that are not available (or have limited availability) to those from other PICES member countries. Ms. Tracy Shaw established the personal WG 23 page on ZOTERO; she also did a live demonstration of how to access the site over the internet, and showed members how to view the content. Presently there are ~ 125 references listed on the site. David Checkley mentioned that they had tried to use ZOTERO in SPACC at the recommendation of Dr. Patricio Bernal but they never got going on the idea.

AGENDA ITEM 3
Country reports

Detailed reports were presented by Japan, Korea and Russia. Each report summarized work carried out during the past year along with a comment on status of posting references to ZOTERO and the potential for future collaboration on research cruises.

a. Canada
No report.

b. China
No report.

c. Japan
Attempts to improve krill biomass estimates from the MOHT were described and were reported on a poster presented at PICES-2011. A major feeding experiment was carried out in June 2010 during which grazing by krill and copepods was measured. Clearance rates for krill ranged from 54 to 736 ml per euphausiid-hour. Highest filtration rates were on "flagellates". There are more than 100 papers published by Japanese scientists on krill that will soon be posted to ZOTERO. Sixty-four papers are in English with about an equal number in Japanese. What remains is to translate at least the abstract, figure captions and table legends of the more important papers written in Japanese.

d. Korea
Future cruises have been scheduled for April and August 2012–2015. They could include collaborators. Bi-monthly time series of zooplankton data from 1976 show a gradual increase in zooplankton biomass since

1990 but copepod biomass has declined since 2005. Recent increases in biomass are due to increased biomass of salps. A total of approximately 30 on-board live-animal experiments were conducted during cruises in 2010 and 2011. The brood size of *E. pacifica* was studied, and research on krill diets based on lipid, stable isotope, and gut content was summarized. On two cruises specimens were collected for genetic analysis and were sent to the Peterson lab in Newport, Oregon. During the April 2011 cruise, plankton net sampling was carried out along with an acoustic survey to derive better estimates of krill biomass. Tracy Shaw (U.S. member of WG 23) participated in the August 2011 cruise.

e. Russia

A summary of the work done by TINRO-Center from 1985–2010 was described. Thousands of plankton samples have been collected and processed for biomass of krill and other zooplankton. Information was presented on the catchability of different plankton nets, which is necessary to understand so that samples collected by different nets can be compared. Overviews of sampling in four regions were provided including the total quantity of zooplankton, the role of every taxonomic group in the structure of plankton community, the species composition and some information about their biology, features of their spatial distribution, vertical distribution, seasonal and inter-annual dynamics of the abundance of major groups, standing stocks of zooplankton and estimates of the volumes of zooplankton consumed by nekton. A list of papers by Russian scientists that could be added to the ZOTERO web-site was provided.

f. U.S.A.

The report from the U.S.A. was in the form of a talk by Tracy Shaw on the synthesis paper, "*Comparison of brood sizes of Euphausia pacifica, pan-Pacific*". This talk generated a debate about the degree to which krill were more like fishes than copepods, as suggested by Dr. David Checkley and Peterson. Dr. Sonia Batten described krill as being like chickens. Dr. Peterson reported briefly on progress of a study of the population genetics of krill. A graduate student has begun to sequence the DNA of *Euphausia pacifica* specimens from Korea and Oregon. Results will likely be reported at PICES-2012 in Hiroshima, Japan.

AGENDA ITEM 4

Presentations

Dr. Michael Dagg reviewed feeding behavior of krill with a focus on *Euphausia pacifica* and asked the question, "What is it about feeding behavior that allows *E. pacifica* to populate wide-spread regions of the North Pacific?" He reviewed the literature on several topics including studies of filter feeding (and mesh size of feeding baskets) and gut contents, predatory feeding, the digestive system, gut passage times and assimilation efficiency. Overall, he concluded that *E. pacifica* is able to eat just about anything (phytoplankton, microzooplankton, mesozooplankton, detritus including marine snow and phytodetritus, and perhaps benthos), within a broad size range from small (a few mm) to large (copepods) and over a very wide range of concentrations – its feeding behavior is flexible, adaptive, and opportunistic. Because it has such dietary flexibility and also has the ability to feed over a very wide range of food concentrations, it is seldom starving, but because it has such high upper levels of ingestion it is seldom satiated or 'full' (*i.e.*, it is almost always at least a little hungry).

Xiuning Du is a Ph.D. student from Ocean University in Qingdao, China, who worked in Dr. Peterson's lab in Newport for 1½ years. Among other things, she performed experiments on grazing by adult *Euphausia pacifica* using the "disappearance of particles" technique, both through microscopic counts and "disappearance of chlorophll" using size-fractionation of natural seawater and fluorometry. A summary of her work is as follows: selective feeding does occur in *E. pacifica*. Long-chain diatoms were sometimes avoided when they had especially high density. As for diatom prey, adaptive and opportunistic feeding could be seen; ciliates were the preferential prey when they had substantial biomass before the upwelling season or during the decay of upwelling blooms. In the late upwelling season in August, ciliates were preferred though in low abundance, likely because of opportunistic feeding or seasonally physiological needs like essential nutrients. Smaller flagellates were positively selected when better foods were lacking. Large dinoflagellates or ciliates were predominantly preferred to their smaller types. Questions were centered on the significance of "selectivity".

AGENDA ITEM 5
General Discussion

There was interest by everyone in continuing the Working Group activities, especially the collaborations that have been established. The members present also felt that it would be useful to try to establish a new working group. It was suggested that the Working Group Final Report could be used to introduce a new set of questions that would form the basis of the new working group. WG 23 resolved to continue discussions on the potential of forming a new working group that would focus on one of two topics: (a) euphausiid vital rates, a topic needed to improve models – will require new experimental work, (b) basin-scale comparison of the role small pelagics in ecosystems (krill, anchovies and sardines) and how their roles might by modified by a changing climate – will require some new thinking.

WG 23 Endnote 1

WG 23 participation list

Members	Observers
Michael J. Dagg (U.S.A.)	Sonia Batten (Canada, representing David Mackas)
Natalia Dolganova (Russia)	David Checkley (U.S.A.)
Se-Jong Ju (Korea)	Vladimir Kulik (Russia)
Yuji Okazaki (Japan)	Ryan Rykaczewski (U.S.A.)
C. Tracy Shaw (U.S.A.)	
William T. Peterson, (U.S.A., Co-Chairman)	

WG 23 Endnote 1

WG 23 meeting agenda

10. Welcome and introduction
11. Agenda additions and/or changes
12. Status of posting references and papers
13. Country reports
14. Presentations (M. Dagg, X. Du)
15. General discussion

Appendix 5

PICES Press Article

Krill Biology and Ecology Workshop

by William Peterson, Jaime Gómez-Gutiérrez, Angus Atkinson and Bettina Meyer

The final official gathering of the international GLOBEC scientific community was held from June 22–26, 2009, in Victoria, British Columbia, Canada, at the Victoria Conference Center, a venue well known to most PICES scientists. The five-day meeting included 10 workshops on the first two days followed by three days of invited and contributed talks and posters. This report summarizes activities at the two-day workshop on "*Krill Biology and Ecology in the World's Oceans*" co-convened by the authors of this article.

The idea for this workshop originated at a workshop with a similar title that was held at the PICES/ICES/GLOBEC 4th Zooplankton Production Symposium in May 2007, in Hiroshima (Japan). More than one hundred krill enthusiasts at this workshop endorsed the need to meet more regularly, thus Drs. So Kawaguchi and Bill Peterson proposed to GLOBEC that another workshop be held at the 3rd and final GLOBEC Open Science Meeting. The proposal was approved and planning began in earnest. The Victoria workshop marked the sixth time that krill biologists had assembled for the specific purpose of discussing krill biology and ecology, with the first two being held in Wilmington (North Carolina, U.S.A.) and Bremerhaven (Germany) in 1982 and 1983. After a long pause, regular gatherings took place with the third and fourth meetings in Santa Cruz (California, U.S.A.) in 1999 and Nagoya (Japan) in 2002. The Hiroshima meeting was the fifth. Discussions are underway to propose a seventh meeting in Pucón (Chile) as part of the forthcoming PICES/ICES 5th Zooplankton Production Symposium to be convened in 2011.

Krill Biology and Ecology Workshop in session.

The purpose of the krill workshop was fourfold. Firstly, the conveners recognized the need for those working on different euphausiid species to get together to discuss methods/approaches that have proved effective for one species to see if they could be applied to other euphausiid species. Secondly, we wanted to make sure that there was a degree of harmony (or at least that there was no serious disconnect) in research approaches, recognizing the need to improve technical aspects of specific methods where necessary. Thirdly, we wanted to generate ideas for future collaborations (laboratory/seagoing exchanges of personnel and exchange and pooling of datasets to address broad-scale issues). Finally, we proposed to produce a tangible product, to show where krill research is at the moment, and to identify hurdles to progress and potential solutions. It was agreed that "the krill workshop group" will produce a summary paper for consideration of publication in the *Marine Ecology Progress Series*.

Towards these ends, on the first day (June 22), 16 presentations were made which summarized national programs – 9 talks on work in the Antarctic mostly focused on the Antarctic krill *Euphausia superba* by scientists from the UK, Germany, Australia, Korea and the USA and 7 talks on work carried out in the Pacific (in Peru/Chile, Mexico, USA, Canada, Japan, China and Korea). At least five common themes emerged from the discussions:

1. The biomass of all krill species has likely been underestimated, and thus there is a need to make better use of acoustics and large plankton nets in order to derive proper estimates of krill biomass;
2. We need to gain a better appreciation of the role of krill as predators and prey in marine food webs, especially with regards to krill as a "wasp-waist" species (*e.g.*, *Euphausia superba*, *E. pacifica* and *Meganyctiphanes norvegica*) – by definition, such species occupy an intermediate trophic level that is strongly dominated by a single species with large fluctuations in biomass such that their prey and predators are measurably impacted by the large swings in biomass;
3. We only have a very rudimentary knowledge of krill behavior and the factors which result in krill forming schools, aggregations and patches at multiple time–space scales and its role in energy cost, physiological adaptation mechanisms to a strong seasonal environment such as the Southern Ocean, species condition and parasite transmission;

4. We need much more pan-oceanic research which will allow us to work out the impact of climate variability and change on krill ecology and production at different latitudinal ecosystems – on this topic, there is abundant evidence that the Antarctic waters are warming and that the ice sheet is melting, two processes that are certain to impact krill but in ways that we can only guess; and
5. Vast improvements have been made using IBM models linked with ROMS (Regional Ocean Model System) to gain a better understanding of krill population dynamics and of how eggs of broadcast spawning species and larvae are transported as a result of interaction of currents with ontogenic variations in vertical distributions.

Talks were supplemented by 17 posters that summarized topics such as larval development and growth, maturation, secondary production, parasitism, analysis of exploitation strategies, effect of global warming, grazing rates, variations in digestive enzymes, lipid trophic markers and larval drift modeling in different regions in the Southern Ocean and Pacific Ocean.

The second day (June 23) included talks on four hot topics such as novel uses of bottom mounted upward facing echo-sounders and high-speed video systems to study krill behaviour and hydrodynamics of swimming and krill patchiness, estimation of mortality rates of *Euphausia pacifica*, and a comparison of the role of krill as prey in the Antarctic and North Pacific ecosystems. The remainder of this day was devoted to discussions of the structure of a synthesis paper that will be prepared for the *Marine Ecology Progress Series*. This will be one tangible output from the workshop, in which we will introduce krill as "wasp-waist" species in important productive ecosystems around the world. The paper will highlight recent developments and issues in krill biology, improving our understanding of how this group fit into their ecosystems.

Perhaps 50 people from at least 11 nations attended the workshop for the two full days whereas another 50 attended one or more of the talks on the first day. Members of the PICES Working Group on *Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim* were well represented by talks by Bill Peterson, Dave Mackas, Yuji Okazaki, Song Sun, Hyoung Chul Shin, Leah Feinberg and Jarrod Santora.

The workshop was concluded by a power point presentation prepared by Dr. Jaime Gómez-Gutiérrez which honored the life-time achievements of three distinguished krill biologists, Edward Brinton and Margaret Knight (from Scripps Institution of Oceanography) and John Mauchline (from the Scottish Association of Marine Science, Oban, Dunstaffnage Laboratory). Each received a "commemorative diploma", a copy of a krill video and a fetching krill "paper weight" made by Lisa Roberts (see below). Each of these scientists was a pioneer in early work on krill: Ed Brinton for work on zoogeography, taxonomy and ecology of krill throughout the Pacific Ocean; Margaret Knight for work on krill larvae taxonomy, including descriptions of the larvae of 13 euphausiid species, and John Mauchline for his research and periodic landmark reviews in *Advances in*

Three legends in their young careers studying euphausiids: Left: Edward Brinton at Scripps working on his Ph.D. research; Center: Historic picture of seven distinguished krill biologist in the early 1970s, from left to right A.C. Baker, Brian Boden, Tarsicio Antezana, Elizabeth Kampa, Edward Brinton, K. Gopalakrishnan, and John Mauchline at San Diego California; Right: Margaret Knight working at Scripps Institution Oceanography. Photos provided by Margaret Knight, Tets Matsui, Annie Townsend, Elizabeth Venrick, and SIO Publications.

*Edward Brinton setting up a MOCNESS net in the Southern Ocean (*circa *1991), Margaret Knight and John Mauchline (recent pictures). Photos provided by SIO Publications, Margaret Knight, and Glen Claxton.*

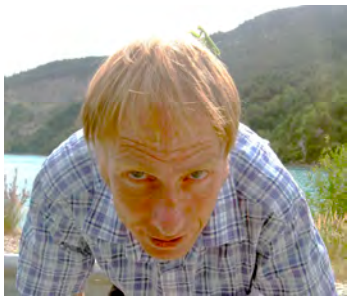
Marine Biology on the biology and ecology of krill worldwide still considered core texts of euphausiid biology. Tarsicio Antezana (Chile) had the original idea to do this tribute and wrote an informal, sometimes humoristic, poetic text to remember the legacy of Ed and Margaret. Unfortunately our friend Tarsicio was unable to attend the workshop.

The workshop included some outreach materials produced by Lisa Roberts, a Ph.D. student from College of Fine Arts, University of New South Wales, who produced both our "krill logo" and an animation named *Antarctic Energies* which was shown during the workshop breaks and during the poster session. Lisa's delightful and fascinating videos can be viewed at http://www.antarcticanimation.com/content/animation/energies/energies.php. The video *Antarctic Energies* was inspired by Lisa after she traveled to the Southern Ocean on board the R/V *Aurora Australis* and saw schooling krill alive in the Australian Antarctic Division Krill Laboratory in Tasmania and heard the insights of scientists who breed them.. *Antarctic Energies* represents physical and biological forces that interact to shape Antarctica: diatoms, krill, sea butterflies (pteropods), seals, albatrosses, humans, sea ice, bottom water circulation, the circumpolar current, ice melting, and sea level rising. Feel free to contact her (lisa@lisaroberts.com.au) or see her webpage at http://www.lisaroberts.com.au/.

A "Krill logo" designed by Lisa Roberts.

An evening social at the Irish Times pub was attended by about 50 krill biologists and ecologists, where many krill stories were exchanged by all, but most importantly, new, exciting and fruitful collaborations were established. Without a doubt, these two days were truly an unforgettable bonding experience for everyone.






Dr. William (Bill) Peterson (bill.peterson@noaa.gov) is an oceanographer and zooplankton ecologist at the Hatfield Marine Science Center in Newport, Oregon. He works for NOAA's National Marine Fisheries Service, and his research focuses on climate effects on zooplankton, particularly euphausiids and copepods. Recently his lab has made advances in the business of forecasting the return rates of salmon to their natal streams one year in advance. Within PICES, Bill has served on several expert groups and is currently a member of the Biological Oceanography Committee and Co-Chairman of the Working Group on Comparative Ecology of Krill in Coastal and Oceanic Waters around the Pacific Rim.

Dr. Jaime Gómez-Gutiérrez (jagomezg@ipn.mx) is a Biological Oceanographer at Centro Interdisciplinario de Ciencias Marinas (Instituto Politécnico Nacional) at La Paz B.C.S., Mexico. His research focuses on the biology and ecology of zooplankton and micronekton in the epipelagic ecosystem, particularly studying since 1990 euphausiid diel vertical distribution with hydroacoustic and submarine video cameras, secondary productivity, ecophysiology, and parasitism. He was part of the 15 authors of the PICES Science Report No. 30 entitled: Micronekton of the North Pacific. During 2008-2009 he did a sabbatical research at the Australian Antarctic Division at Kingston Tasmania, Australia working on a review of euphausiid parasites with Steve Nicol and So Kawaguchi. He did a PhD thesis at Oregon State University working in several GLOBEC research projects studying euphausiid embryonic development rates, hatching mechanisms, reproductive effort, and parasitism of Euphausia pacifica and Thysanoessa spinifera along the Washington-Oregon-California coasts.

Dr. Angus Atkinson (aat@bas.ac.uk) works at the British Antarctic Survey in Cambridge, UK. He is fond of all kinds of invertebrates (even terrestrial ones – see photo), but his real love is Antarctic krill. He started working on krill by accident in 1996 (there were not any amphipods to work on but loads of krill instead) and has worked on them ever since. Topics include feeding, excretion, defecation and growth, and more recently large scale distribution. All of this involves a healthy amount of labwork and experimentation on live animals, and Angus has now participated in 15 Antarctic cruises.

Dr. Bettina Meyer (bettina.meyer@awi.de) is a Marine Biologist at the Alfred-Wegener Institute of Polar and Marine Research (AWI, Germany). She worked on trophic interaction and the seasonal variability in ecophysiological condition on planktonic crustaceans. Since 1999 her research focuses on the physiology of Antarctic krill, the mechanisms causing synchronization between the seasonal development of krill and the seasonal cycles of environmental features in particular. She has been initiated the LAKRIS project (Lazarev Sea Krill Study), the German contribution to the Southern Ocean GLOBEC program.

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Continued on inside back page

PICES PUBLICATIONS

The North Pacific Marine Science Organization (PICES) was established by an international convention in 1992 to promote international cooperative research efforts to solve key scientific problems in the North Pacific Ocean.

PICES regularly publishes various types of general, scientific, and technical information in the following publications:

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ABSTRACT BOOKS – are prepared for PICES Annual Meetings and symposia (co-)organized by PICES.

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Front cover figure

Top row: *Euphasia pacifica* – unhatched nauplius, hatching nauplius, calyptopis. Second row: *E. pacifica* male, *E. pacifica* adult with green phytoplankton in the hepatopancreas. Third row: *Thysanoessa spinifera* adult, *T. spinifera* adult with molt. Bottom row: two images of *E. pacifica* females with purple ovaries, indicating that they are ready to release eggs. Photo credits: Jaime Gómez-Gutiérrez and C. Tracy Shaw.